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A STUDENTS'

TEXT-BOOK OF BOTANY

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TEXT-BOOK OF BOTANY

BY

SYDNEY H. VINES M.A., D.Sc., F.R.S.

Fellow of Magdalen College and Sherardian Professor of Botany in the University of Oxford; formerly Fellow of Christ's College and Reader in Botany in the University of Cambridge; Fellow of the University of London

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PREFACE.

When, some few years ago, it became necessary to revise the English Edition of the late Prof. Prantl's *Lehrbuch der Botanik*, it appeared to me that the requirements of English students would be more satisfactorily met if the scope of the work were so extended that, whilst retaining all that has made it of value to beginners, it might be more useful to those engaged in the advanced study of the science. With this object in view, the number of pages has been doubled by additions to all four parts of the book, but more especially to Part III. dealing with the Classification of Plants.

Though the form of Prof. Prantl's book is still retained, and here and there paragraphs from the English edition have been inserted, the present is essentially a new and distinct work for which I alone am responsible, and, consequently, on the title-page of which my name alone appears.

I would most gratefully acknowledge the assistance which I have received from my friend Dr. D. H. Scott, F.R.S., Honorary Keeper of the Jodrell Laboratory, Royal Gardens, Kew, who has kindly read the proofs, and has furnished me with many valuable suggestions and criticisms. The usefulness of the book is enhanced by the incorporation of a number of additional illustrations: most of these are placed at my disposal by the publishers, from their English edition of Prof. Strasburger's *Practical Botany*; a few are taken from various other sources which are duly acknowledged.

S. H. V.

ERRATA.

Page 8, line 10 from bottom, for *of* read *or*.
,, 9, in description of Fig. 2, for *zygomorphic* read *isobilateral*.
,, 29, line 6 from bottom, *Marsilia* should be spelt *Marsilea* throughout.
,, 44 ,, 12 ,, ,, for *othostichies* read *orthostichies*.
,, 60 ,, 11 ,, ,, for *inbricate* read *imbricate*.
,, 61 ,, 17 ,, top, for *tranverse* read *transverse*.
,, 67 ,, 5 ,, bottom, for *Mucorini* read *Mucorinæ*.
,, 69 ,, 16 ,, ,, the bracket should follow the word *intine*.
,, 90 ,, 12 ,, ,, omit *that*.
,, 106 ,, 16 ,, ,, for *chor-zinc-iod* read *chlor-zinc-iod*.
,, 117 ,, 14 ,, ,, for *mother-cels* read *mother-cells*.
,, ,, ,, 4 ,, ,, for *mother-ces* read *mother-cells*.
,, 121 ,, 3 ,, ,, for *Gingko* read *Ginkgo*.
,, 127 ,, 3 ,, top, for *Schizeaceæ* read *Schizæaceæ*.
,, 162 ,, 21 ,, bottom, for *that is, are perpendicular* read *that is, are parallel*.
,, 173 ,, 14 ,, top, for *other* read *outer*.
,, 176 ,, 2 ,, bottom, for *protohploem* read *protophloem*.
,, 182, in description of Fig. 139, for *Kortex* read *Cortex*.
,, 240, line 8 from bottom, omit *Chlorodictyon*.
,, ,, ,, 5 ,, ,, omit *Codiolum marine*.
,, 249 ,, 27 ,, ,, for *germinates* read *germinate*.
,, 265, in description of Fig. 191, for *oospores* read *oospheres*.
,, 276, line 9 from top, for *asocarp* read *ascocarp*.
,, 308, in description of Fig. 218, for *spondia* read *sporidia*.
,, 345, *et passim*, for *Symphogyna* read *Symphyogyna*.
,, 368, in description of Fig. 250, for *seratum* read *serratum*.
,, 372, line 6 from top, *conspicious* read *conspicuous*.
,, 375 ,, 20 ,, bottom, for *te* read *to*.
,, 462 ,, 15 ,, ,, for *Class I.* read *Class VIII.*
,, ,, ,, 4 ,, ,, for *Class I.* read *Class IX.*
,, ,, ,, 2 ,, ,, for *Class II.* read *Class X.*
,, 463 ,, 2 ,, top, for *Class I.* read *Class VIII.*
,, 489 ,, 6 ,, ,, omit *Class II.*
,, 509 ,, 12 ,, bottom, for *Ribes alpina* read *Ribes alpinum*.
,, 543 ,, 8 ,, ,, for *Fam.* 1 read *Fam.* 3.
,, 591 ,, 7 ,, ,, for *inconspicucous* read *inconspicuous*.
,, 611 ,, 5 ,, top, for *Theobromo* read *Theobroma*.
,, ,, ,, 7 ,, ,, for *ola* read *Cola*.

CONTENTS.

PART I.—THE MORPHOLOGY OF PLANTS.

CHAPTER I.—GENERAL MORPHOLOGY.

CHAPTER II.—THE SPECIAL MORPHOLOGY OF THE MEMBERS.

A. Vegetative Organs.

B. Reproductive Organs.

PART II.—THE INTIMATE STRUCTURE OF PLANTS.

(Anatomy and Histology).

CHAPTER I.—THE CELL.

CHAPTER II.—THE TISSUES.

PART III.—THE CLASSIFICATION OF PLANTS.

PART IV.—THE PHYSIOLOGY OF PLANTS.

CHAPTER I.—GENERAL PHYSIOLOGY.

CHAPTER II.—SPECIAL PHYSIOLOGY OF THE NUTRITIVE FUNCTIONS.

CHAPTER III.—SPECIAL PHYSIOLOGY OF MOVEMENT.

CHAPTER IV.—SPECIAL PHYSIOLOGY OF REPRODUCTION.

GROUP IV.

PHANEROGAMIA (OR SPERMAPHYTA).

THESE are all heterosporous plants, having a definite alternation of generations, which is, however, not readily perceived on account of the great reduction of the sexual generation, and of the fact that the female gametophyte remains enclosed in the macrospore, that the macrospore remains enclosed in the macrosporangium, and that the macrosporangium remains for a long time attached to the sporophyte, the result being the development of a *seed* which constitutes a characteristic feature of the group (see p. 217).

A. THE SPOROPHYTE. As in the Pteridophyta, so here, the plant itself is the sporophyte or asexual generation.

It is unnecessary to go into detail at present with regard to the morphology of the vegetative organs; full information is given in the section on General Morphology, and subsequently in the description of the classes and orders.

The *Reproductive Organs* of the sporophyte are sporangia of two kinds, microsporangia and macrosporangia, which are usually borne on sporophylls, but sometimes directly on the axis: the modified shoots bearing the sporangia constitute *flowers*; and they usually bear, in addition to the sporophylls, other floral leaves (hypsophylls, see p. 79), protective or attractive in function, some of which usually constitute a perianth.

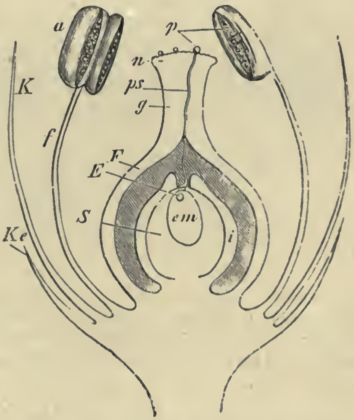

FIG. 260.—Diagram of an angiospermous flower. *Ke* Calyx. *K* Corolla; *f* filament of stamen; *a* anther with two pollen-sacs in each half which are opened, showing the pollen-grains (*p*). These fall on the stigma, and the pollen-tube (*ps*) penetrates the style (*g*) as far as the cavity of the ovary (*F*), reaching the ovule (*S*); *i* the integument of the ovule; *em* the embryo-sac. *E* The oosphere.

The flowering shoot constitutes an *inflorescence*, which may consist of one or many flowers, according to the extent to which the shoot branches.

The *Flower* (see p. 76) is a sporangium-bearing shoot or sporophore with usually undeveloped or feebly developed internodes, so that the sporophylls and hypsophylls which it bears are closely aggregated together. Most commonly the flower is ambisporangiate (monoclinous, or hermaphrodite), but it is frequently monosporangiate (unisexual): in the latter case there are two kinds of flowers, microsporangiate and macrosporangiate, which may be borne by the same individual, when they are said to be diclinous and monœcious; or by two distinct individuals, when they are diœcious (see p. 86). Occasionally the same plant produces both ambisporangiate and monosporangiate flowers, when it is said to be *polygamous.* The microsporangiate flowers are frequently termed *staminate,* and the macrosporangiate flowers *carpellary* (p. 78): the former are indicated by the sign ♂, the latter by the sign ♀, and ambisporangiate flowers by the sign ☿. In the Gymnosperms the flower is always monosporangiate; in the Angiosperms it is generally, though by no means always, ambisporangiate. The flower of the Gymnosperms is nearly always destitute of a perianth.

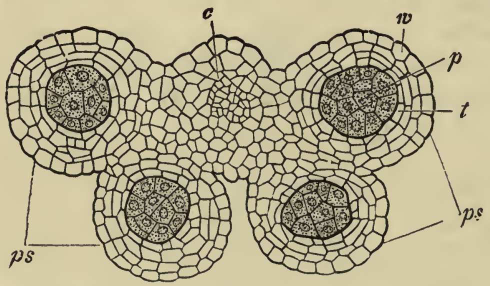

FIG. 281.—Transverse section of a young anther of *Sambucus racemosa* (×80): *c* the connective with the vascular bundle; *ps* the four pollen-sacs (microsporangia); *p* the mother-cells of the pollen; *t* tapetal layer; *w* the wall of the pollen-sac.

The special morphology of the *Perianth* is dealt with under the Angiospermæ, in which class it attains its highest development.

The *Sporophylls* are of two kinds: *microsporophylls,* otherwise known as *stamens*; and *macrosporophylls,* otherwise known as *carpels*: the former bear exclusively microsporangia, the latter exclusively macrosporangia. The sporophylls present considerable variety of form, and are on the whole more highly specialised than in any of the Pteridophyta.

The *microsporophyll,* or stamen (see p. 78), in its most highly specialised form, consists of a stalk of varying length, the *filament,* bearing a terminal structure, the *anther,* which is a sorus of one or more microsporangia embedded in more or less placental tissue. In the less highly organised Phanerogams (*e.g.* most Gymnosperms), the microsporophylls are morphologically simpler, having the general character of sessile or shortly-stalked scaly leaves.

The *macrosporophyll*, or carpel, bears (usually) macrosporangia (see p. 78). In the Angiosperms the carpel, either by itself or by cohesion with others, forms a closed cavity, the *ovary*, which is frequently prolonged at its apex into a longer or shorter process, the *style*, bearing at its summit a glandular surface, the *stigma*: sometimes the style is absent, so that the stigma is sessile on the ovary; within the ovary the macrosporangia are developed. In the Gymnosperms, the macrosporophylls (when present) do not cohere, either individually or several together; so that in this group there is no ovary, style, or stigma; they are thus distinguished from the Angiosperms, in which there is always an ovary.

The *Sporangia* are of two kinds; *microsporangia* or *pollen-sacs*, and *macrosporangia* or *ovules*. The development of the sporangium is, in both, eusporangiate (see p. 73). The sporangia are, as a rule, borne on the sporophylls; but in some few cases (*e.g.* microsporangia of Naias, Casuarina; macrosporangia of Taxus, Polygonum, Primulaceæ, etc.) they are borne on the axis.

The *microsporangia*, or pollen-sacs, may be developed either singly or in a sorus of two or more; they may be very numerous on the sporophyll, as in the Cycadaceæ. When borne on the sporophylls, they are developed on the lower (dorsal) surface of the microsporophyll in the lower forms (*e.g.* Cycadaceæ, Coniferæ); whereas in the Angiosperms they are usually developed both on the upper (ventral) and the lower surfaces.

The microsporangia either project freely or are embedded in the placental tissue of the member bearing them. The multicellular hypodermal archesporium is either a row or a layer of cells. The archesporial cells undergo, as a rule, division, giving rise to the sporogenous cells together with a more or less extensive transitory layer of investing cells, the *tapetum*, which is eventually disorganised.

The microsporangium is, as a rule, unilocular; but in a few Angiosperms some of the sporogenous cells are sterile and, instead of giving rise to spores, constitute walls which render the microsporangium multilocular. The septa are either transverse, so that the loculi are in a vertical row (*e.g.* species of Mimoseæ; also some Onagraceæ, such as Circæa, Gaura, Clarkia); or both transverse and longitudinal, as in Rhizophora and Viscum.

The microsporangium eventually dehisces, generally by a longitudinal slit, less commonly by a transverse slit or by a pore.

The dehiscence is mainly effected by a layer of tracheidal cells, differentiated as part of the wall, which are highly hygroscopic.

The *microspores*, or pollen-grains, are developed from the sporogenous mother-cells of the sporangium. As a rule each mother-cell divides so as to give rise to four microspores, all of which develope. As a rule, also, the microspores eventually become quite free from each other, but to this there are exceptions: thus, in the Mimoseæ, while the pollen-grains are isolated in some species, in other species they cohere in groups of 4, 8, 12, 16, or 32, derived from one, two, three, or more mother-cells; again, in the Orchidaceæ, whilst Cypripedium has isolated pollen-grains, in most genera the pollen-grains are in groups of four (tetrads), and cohere into a mass (or 2–8 masses), the *pollinium*, of varying consistence (see Orchidaceæ): pollinia also occur in the Asclepiadaceæ.

The microspore has, as a rule, the ordinary structure of a spore (see p. 69); it is a nucleated cell, with a certain amount of granular nutritive material in its cytoplasm, and has two coats, an intine and an exine, the structure of the latter being elaborate in many cases. The spore has not, however, always two coats. In some plants there is no exine, and only a single thin coat, as in the cells of the pollinia of Orchids and Asclepiads, and in certain plants whose flowers develope under water, such as certain Naiadaceæ (Zostera, Posidonia, Cymodocea, Naias), in Halophila (Hydrocharidaceæ), and in some species of Callitriche. In others, again, there is but one coat, but it is thick and is cuticularised externally (*e.g.* Senecio), or the two coats are only distinguishable at those points at which the pollen-tubes will be eventually protruded (*e.g.* Onagraceæ, Cobæa).

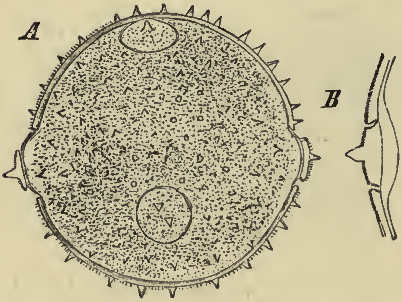

FIG. 282.—*A* Pollen-grain of *Cucurbita Pepo*, showing the lid-like areas through which the pollen-tubes will protrude (×240). *B* Section of one of these areas (×540: after Strasburger).

The exine is frequently highly differentiated with special reference to the protrusion of the pollen-tubes: it may be porous (*e.g.* Malvaceæ, Fig. 283); or there may be thin areas at certain points; or (Onagraceæ) much-thickened areas where the pollen-tubes are eventually developed; or, again, areas are marked off here and there which come off like lids under the pressure of the developing pollen-tube (Fig. 282).

The development of the microspores has already been dealt with in general (see p. 125), so that it will be only necessary here to mention certain special points. In the first place there is an exception to the rule that each mother-cell gives rise to four microspores; in Asclepias each mother-cell developes directly, without division, into a cell of the pollinium, each such cell being, at any rate physiologically, equivalent to a microspore; apparently the same is the case in Zostera where, however, the microspores are isolated. The mother-cells of the microspores either remain coherent, during the development of the microspores, or (as in many Monocotyledons) they become free and float in the granular fluid, derived from the disorganisation of the tapetum, which fills the pollen-sac. The walls of the mother-cells usually become very much thickened, especially in the planes of the future

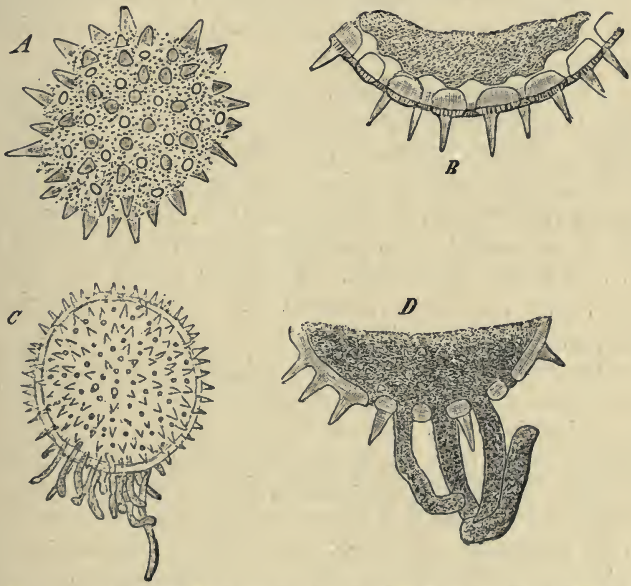

FIG. 283.—Pollen-grains of *Malva crispa*. *A* Grain seen from surface; *B* section of wall, showing the exine with its alternate spines and pores, the latter closed internally by the delicate innermost layer of the exine; *C* germinating pollen-grain with pollen-tubes; *D* the same in section, showing the protrusion of the pollen-tubes through the pores. (*A*, *B*, *D* × 540; *C* × 240: after Strasburger.)

divisions. The division of the mother-cell is either successive (Monocotyledons, Cycads), or simultaneous (most Dicotyledons and Conifers); in the former case the microspores are usually bilateral, in the latter tetrahedral. The form of the mature microspore varies widely; it may be spherical, etc.; in plants in which pollination takes place under water, the microspore becomes elongated and filiform (*e.g.* Zostera, Posidonia, Cymodocea, and to some extent also in Naias), and in Halophila the microspores are aggregated into filaments.

In some cases the germination of the pollen-grain begins before it is set free from the dehisced pollen-sac, so that it consists of two (sometimes more in Gymnosperms) cells at the time of pollination.

The *macrosporangia*, or ovules, are developed singly, or in pairs, or more commonly several together, from a more or less well-developed cushion of tissue, the *placenta.* When the ovules are borne on sporophylls, the placenta is either marginal, or, less commonly, it is ventral, including the whole of the upper or inner surface of the carpel with, sometimes, the exception of the mid-rib (*e.g.* Butomus, Nymphæa). When the ovules are borne on the axis, they are either terminal (*e.g.* Taxus, Polygonum) or lateral (*e.g.* Primulaceæ, Compositæ).

The macrosporangium, like the microsporangium, makes its appearance as a small cellular prominence on the surface of the organ which bears it, formed by the division of a group of hypodermal cells; it is covered at the surface by an epidermal layer which usually remains single, though in some cases (*e.g.* Gymnosperms, Delphinium, Helianthemum, Rosaceæ, *Iris Pseudacorus*) the epidermal cells undergo repeated periclinal divisions and thus add considerably to the bulk of the micropylar portion of the nucellus.

The macrosporangium proper (sometimes distinguished as the *nucellus*) is invested by one or two coats, which grow up from the base, but do not completely close over the apex, leaving there a narrow channel termed the *micropyle*; the base of the macrosporangium, where the coats and the tissue of the sporangium proper become indistinguishable, is termed the *chalaza.* The coats of the ovule in Phanerogams are the morphological equivalent of the indusium in the Pteridophyta, though, in the former the sorus consists of a single macrosporangium; but this is also the case in Azolla, Isoetes, etc., among the Pteridophyta.

The macrosporangium is not, as a rule, embedded in the placental tissue, and is sometimes borne on a longer or shorter stalk, the *funicle.* The point of attachment of the macrosporangium, whether it be sessile or stalked, to the placenta, is termed the *hilum.*

The form of the macrosporangium presents many varieties, of which the following are the more common. When the micropyle, the chalaza, and the funicle (or the hilum) all lie in one and the same straight line, the ovule is said to be *orthotropous*: when the micropyle and the chalaza lie in the same straight line, but not the funicle, the ovule being bent back against the funicle (termed the *raphe* along the line of contact), the ovule is *anatropous*; when the ovule itself is curved, so that the micropyle and the chalaza do not lie in the same straight line, the ovule is *campylotropous.* Various intermediate forms occur which may be easily imagined.

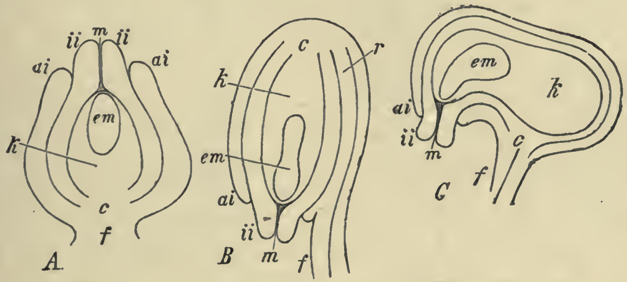

FIG. 284.—Diagrams of the Ovule. *A* Orthotropous. *B* Anatropous. *C* Campylotropous. *f* Funicle; *ai* the outer integument; *ii* the inner integument; *m* micropyle; *k* nucellus; *em* embryo-sac; *r* the raphe; *c* chalaza.

The archesporium (see p. 73), which here, as elsewhere, is hypodermal, consists generally of one cell, though sometimes apparently of several lying side by side (*e.g.* Casuarina; some Rosaceæ, such as *Rosa livida*, *Fragaria vesca*, *Cydonia japonica*, *Sanguisorba pratensis*; possibly also some Gymnosperms, Gnetum, Taxus, Ginkgo, Thuja). In some cases the archesporial cell undergoes no division (*e.g. Tulipa Gesneriana*, *Lilium bulbiferum*) but directly developes into the mother-cell of a macrospore; but, as a rule, the archesporial cell (or cells) undergoes more or less frequent division. Thus, in most Phanerogams, the division of the archesporial cell begins with the cutting off, by a periclinal wall, of a sterile cell towards the organic apex (micropylar end) of the macrosporangium—or sometimes two such sterile cells—which, with or without further division, represent a tapetal layer. The large remaining cell now undergoes division into two by a transverse wall, and one or both of these cells may divide in a similar manner. Thus a longitudinal row of large cells, two to four in number, is formed, all of which are potentially mother-cells of macrospores. In some plants (*e.g.* Senecio and other gamopetalous Dicotyledons; *Orchis pallens*, *Gymnadenia Conopsea*, and some Grasses, among Monocotyledons) no tapetal cells are cut off. In a few plants (Cycads, *Callitris quadrivalvis*, *Cupressus sempervirens*, among Gymnosperms; Casuarina and some other Amentales, among Angiosperms) the growth of the archesporial cells is more extensive, leading to the production of a considerable mass of sporogenous tissue, as in the macrosporangia of the Pteridophyta.

Generally speaking, only one of the cells of the sporogenous tissue shows any sign of developing into a macrospore; and in the normal Angiosperms, this cell is generally the lowest (nearest the chalaza) of the longitudinal row described above. In some exceptional cases (*e.g.* *Rosa livida*, Casuarina, Taxus, Ginkgo, Thuja, Gnetum) several of the potential mother-cells begin, at least, to develope, though even in these cases only one of them, as a rule, ultimately gives rise to a fertile macrospore.

The growth of the fertile mother-cell of the macrospore is vigorous. It causes the displacement and absorption of the sterile cells of the sporogenous tissue. But Casuarina is an exception in this respect; here the numerous (as many as twenty) mother-cells all grow with equal vigour, and, as they do not attain a large size, there is space for them all in the macrosporangium. Casuarina is further peculiar in that some of the small sterile cells of the sporogenous tissue develope into tracheidal cells somewhat resembling the elaters of the Hepaticæ.

The macrosporangium is indehiscent, and only becomes detached from the plant after it has developed into a seed.

The *macrospore* or *embryo-sac* is, as a rule, developed singly in the macrosporangium; and, further, it is always developed singly from its mother-cell without any indication of that division into four which is characteristic of the development of spores in general. It is in fact impossible, as a rule, to fix upon any stage at which the transition from macrospore-mother-cell to macrospore may be considered to take place; for the mother-cell simply grows and becomes the macrospore without any special differentiation. However, in the Cycadaceæ, the wall of the mother-cell undergoes that differentiation which is characteristic of spores, so that the wall of the macrospore consists of two layers the outer of which is cuticularised. The macrospore is simply a large cell, containing vacuolated protoplasm in which lies a nucleus, and having, as a rule, a wall of cellulose.

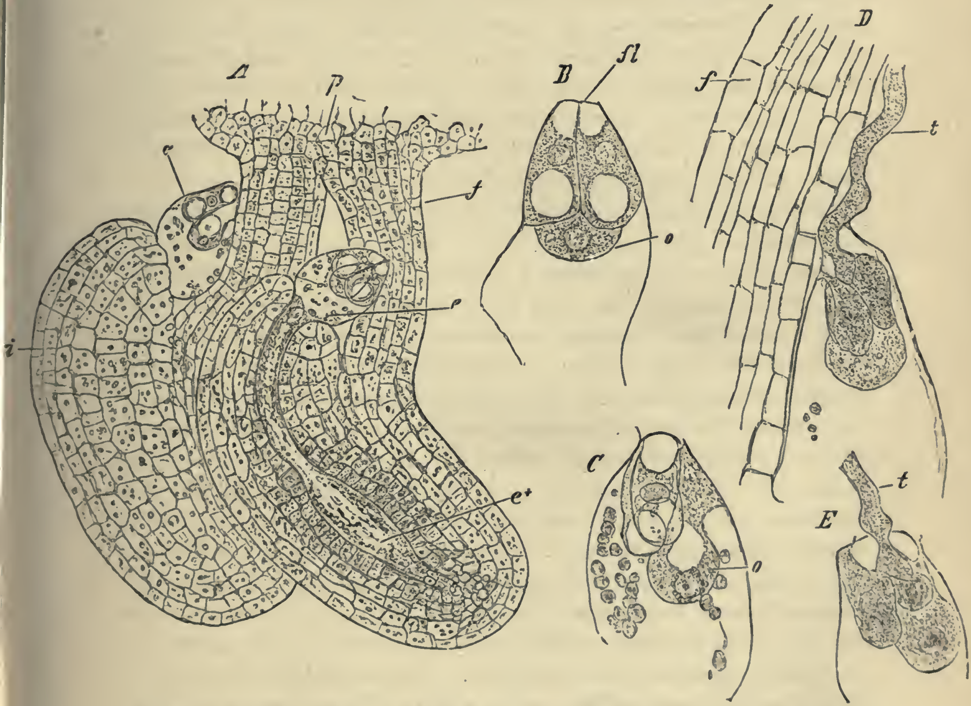

FIG. 285.—*Torenia asiatica.* *A* Two anatropous ovules on the placenta *p*; *e* apex of embryo-sac projecting beyond the micropyle; *e** its broad chalazal end in the ovule; *f* funicle; *i* integument (×240). *B* and *C* Free apex of embryo-sac, with egg-apparatus, before fertilisation; *fl* caps of the synergidæ; *o* oosphere. *D* and *E* The process of fertilisation; *t* the pollen-tube; *f* part of the funicle (×600: after Strasburger).

In the course of its growth, the macrospore frequently causes the absorption of more or less of the tissue of the nucellus, more especially towards the micropylar end. It commonly attains such a size that little or none of the nucellar tissue remains, and it may even project beyond the micropyle (*e.g.* Santalum, *Torenia asiatica*, Fig. 285); and in many gamopetalous Dicotyledons it developes tubular outgrowths, which penetrate into and destroy the tissue of the integument (*e.g.* Rhinanthus, Lathræa, some Labiatæ). In some cases, however (*e.g.* Gymnosperms, Scitamineæ, most Nymphæaceæ, Piper), the macrospore does not grow to such an extent, so that a considerable mass of nucellar tissue is left, which persists to some extent in the seed as *perisperm*, its cells being then filled with nutritive substances. This may be due, as in the Gymnosperms, to the fact that the macrospore is covered, towards the micropyle, by a mass of nucellar tissue formed by the growth and repeated division, both periclinal and anticlinal, of either the tapetal cell, or of the apical epidermal cells of the ovule, or of both; or, as in the other cases, to the fact that the macrospore, in its growth, which is relatively slight, does not absorb the chalazal portion of the nucellar tissue.

General Histology. The following are the principal characteristic features:—The apical growth of shoot and root is only exceptionally effected by means of a single apical cell: the small-celled meristem of the growing-point of the stem is more or less distinctly differentiated into dermatogen, periblem, and plerome, so that the stem has a true epidermis: the epiblema of the root is either the persistent innermost layer of the original many-layered endodermis (most Dicotyledons, Gymnosperms), or it is the external layer of the cortex (Monocotyledons; see p. 154): stem and root are monostelic, with but few exceptions (p. 152): the vascular bundles of the stem are generally collateral: both root and stem generally present secondary growth in thickness (except Monocotyledons, and a few other cases) by means of a normal cambium-ring (for abnormal cases, see p. 204): the growing-points of the lateral roots are developed from the pericycle of the parent root (see p. 186).

The Embryogeny of the Sporophyte. The sporophyte is developed from the fertilised oosphere in the ovule. The development of the embryo is not continuous, but is in two stages, which may be conveniently distinguished as the *intra-seminal* and the *extra-seminal.* The intra-seminal stage includes the whole of the development which the embryo undergoes during the conversion of the ovule into the ripe seed—that is, during what is known as the "ripening of the seed." The extra-seminal stage includes the development of the embryo which follows the sowing of the seed;—that is, the escape of the embryo from the seed, and the gradual development of the characters of the adult plant. The interval between these two stages may be brief, or it may extend over many years if the seed be kept dry. The "germination" of the seed when sown is simply the resumption of development by the embryo in consequence of exposure to the necessary conditions of moisture, warmth, etc.

In most Phanerogams, each oospore gives rise to a single embryo; but in most Gymnosperms each oospore gives rise to more than one embryo (four or many), thus exhibiting *polyembryony*.

The primary development of the embryo is either holoblastic or meroblastic (see p. 13); meroblastic embryogeny is common among Gymnosperms.

In some exceptional cases (Cycads, Ginkgo, Ephedra) the embryogeny begins with free cell-formation in the oospore (see p. 121).

Generally speaking, the oospore of holoblastic plants divides into two by a transverse wall: the upper of the two cells remains coherent to the micropylar end of the embryo-sac and developes into the suspensor, an embryonic organ which is a characteristic feature of the embryogeny of Phanerogams, which bears at its lower end the other cell, termed the *embryo-cell*, from which the whole or a considerable part of the body of the embryo is developed. In meroblastic plants, the suspensorial cell and the embryo-cell are developed in a somewhat similar though more complicated manner, from the embryogenic portion of the oospore (see Gymnosperms, p. 71).

It is in comparatively few plants that the suspensor contributes nothing to the development of the permanent members of the embryo. This is necessarily the case in those plants (enumerated below) in which no suspensor is developed; it is also the case in some plants in which a suspensor is present (*e.g.* plants with massive suspensors, such as Geranium, Tropæolum, many Grasses; also most Leguminosæ). Here the embryo is developed entirely from the embryo-cell. In some cases (Vicieæ, Coniferæ) the embryo-cell, on the other hand, contributes to the elongation of the suspensor. In many cases, however, the lowest cell of the suspensor contributes in part (*e.g.* Capsella, Fig. 286) or entirely (*e.g.* Alisma, Fig. 287) to the construction of the embryo.

The suspensor may be regarded, in most cases, simply as a temporary organ of the embryo: but it occasionally presents such a degree of independence of growth, that it assumes the character rather of a proembryonic organism, making the embryogeny heteroblastic, than of a mere organ (see p. 14).

The following are noteworthy peculiarities in the morphology and physiology of the suspensor. It is generally a filament consisting of a longer or shorter single row of cylindrical cells, sharply defined from the rest of the embryo: in some cases it consists of several such rows (*e.g.* Glaucium, Vicieæ): in others it is massive (see above), consisting of a number of cells covering the posterior end of the embryo, and not sharply defined from it: sometimes it consists of a single cell (*e.g.* Funkia): in some plants (*e.g.* Vicieæ) the segments of the suspensor are cœnocytic. Rarely, it is differentiated at a relatively late stage of embryogeny (*e.g. Cytisus Laburnum*, and some other Leguminosæ). Its common function is, by its growth, to force the embryo into the nutritive tissue of the seed, and it is usually attached by its upper end to the micropylar end of the embryo-sac: but it is not unfrequently adapted, more particularly when the embryo-sac contains little or no store of nutriment, as an organ of absorption. Thus in some Orchids (*e.g. Anacamptis pyramidalis*, *Platanthera bifolia*, *Orchis latifolia*), the filamentous suspensor grows through the wall of the embryo-sac, and out at the micropyle, reaching the wall of the ovary where it buries itself in the tissue of the placenta, from the cells of which it absorbs nutriment for the embryo attached to its other end in the embryo-sac. Again, in other Orchids (Phalænopsis, Vanda), the primitive suspensorial cell divides longitudinally into six cells which grow out into long filaments, both upwards and downwards, enveloping the embryo but not leaving the ovule, which act as absorbent organs. In Tropæolum, the suspensor produces two lateral branches, one of which bores through the wall of the ovule into the cavity of the ovary, acting as an anchor for the embryo; the other penetrates the wall of the ovule, where it is in contact with the placenta, and, entering the placental tissue, acts as an absorbent organ. In Gnetum the suspensor branches and bears an embryo at the end of each branch. When the suspensor is massive, it is itself a depository of nutrient substances for the use of the embryo.

No suspensor is developed in the following plants: *Pistia Stratiotes*, *Listera ovata*, *Epipactis palustris* and *latifolia*, *Cypripedium spectabile*, among Monocotyledons; *Corydalis cava*, and certain Leguminous plants, such as the Mimoseæ and some Hedysareæ, among Dicotyledons; Ginkgo, among Gymnosperms.

In those plants which have no suspensor, the development of the embryo from the oospore is simple. The oospore divides by a transverse (basal) wall into two; then by a longitudinal wall into four; and then by a second longitudinal wall, at right angles to both the preceding, into eight cells, octants of a sphere: generally speaking, from the half of the oospore next the micropyle the primary root is developed, from the other half the growing-point of the primary stem and the (one or two) primary leaves or cotyledons. The early stages of the embryogeny are essentially the same in those plants in which, though a suspensor is present, it does not contribute to the structure of the embryo, though here it is the embryo-cell that divides into octants.

In those plants which have a suspensor which contributes to the embryo, the embryo-cell is not a complete sphere. It divides, as a rule, into two by a longitudinal wall, then transversely, and then in a plane to both the preceding, into octants; but while

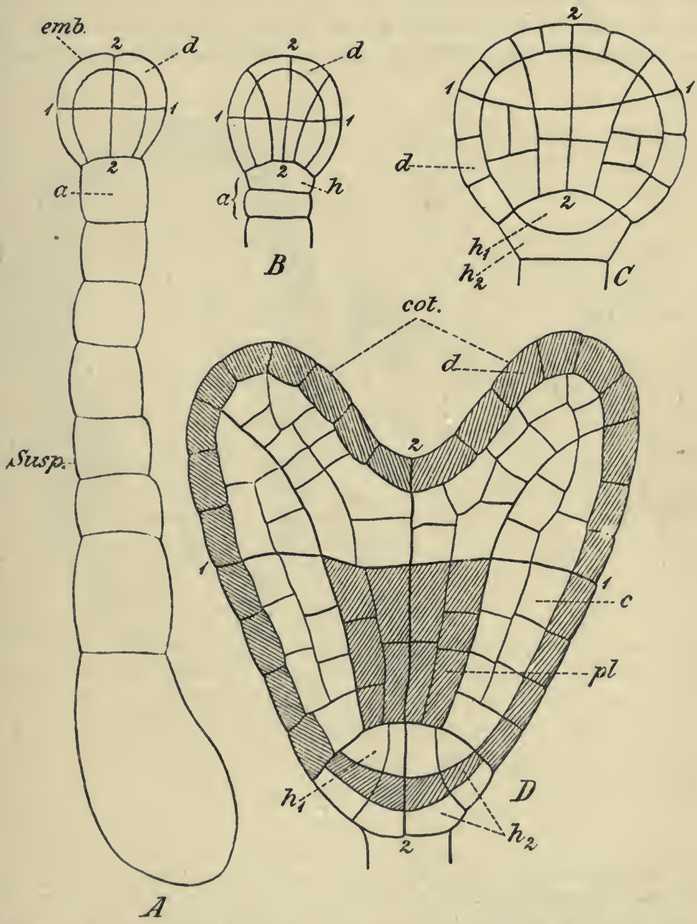

Fig. 286.—Embryogeny of Dicotyledons as represented by *Capsella Bursa-Pastoris* (diagrammatic, after Goebel and Hanstein). *A–D* Successive stages: *susp.* suspensor; *emb.* embryo; 1-1, 2-2, octant-walls; *a* lowest cell of suspensor, dividing in *B* to form the hypophysial cell *h*; in *C* the hypophysial cell has divided into two, h_1 and h_2, the former constituting the periblem, the latter the dermatogen, of the growing-point of the primary root; in *D*, h_2 has undergone a periclinal division to form the primitive root-cap: *d* dermatogen; *c* periblem; *pl.* plerome; *cot.* cotyledons, between which lies the growing-point of the primary stem.

the four anterior octants are octants of a sphere, this is not the case with the four truncated posterior octants abutting on the suspensor. In some cases, the transverse division precedes the longitudinal. From the anterior octants are developed, in Dicotyledons generally (Fig. 286), the two cotyledons and the growing-point of the primary stem, but the growing-point of the primary root is supplied from the last cell of the suspensor (Fig. 286 *A*, *a*) which divides transversely into two (Fig. 286 *B*) and contributes the cell *h*, the *hypophysis*, to complete the root-end of the

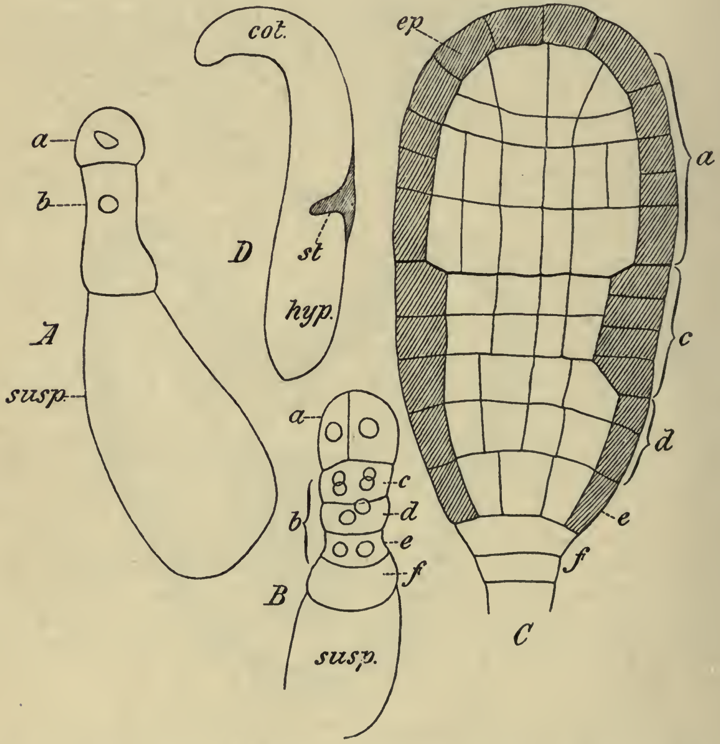

FIG. 287.—Embryogeny of Monocotyledons, as represented by *Alisma Plantago* (diagrammatic, after Goebel, Hanstein, and Famintzin). *A–C* Successive stages: *a* embryo-cell; *b* lowest cell of suspensor, *susp.*: the products of the repeated transverse division of *b* are indicated (*c*, *d*, *e*, *f*) in *B* and *C*. In *C*, *a* has given rise to the single terminal cotyledon; *c* to the growing-point of the primary stem; *d* and *e* form the hypocotyl; the growing-point of the root is developed from *f*; *ep* dermatogen. *D* is a mature embryo, less highly magnified: *cot.* cotyledon; *st.* growing-point of stem; *hyp.* hypocotyl. The nuclei of the cells are indicated in *A* and *B*.

embryo. In Monocotyledons, on the other hand, the embryo-cell gives rise, as a rule (Fig. 287 *A* and *C*, *a*), only to the single terminal cotyledon; whilst the last cell of the suspensor (Fig. 287 *A*, *b*) gives rise to the growing-point of the stem, which is here lateral (Fig. 287 *C*, *c*; *D*, *st*), and to that of the root by a hypophysial cell (*f*).

In two cases only (*Cephalotaxus Fortunei*, *Araucaria brasiliana*, both Gymnosperms) are the cotyledons and the growing-point of the primary stem developed endogenously: here they are at first covered by some cells at the apex of the embryo, which are eventually thrown off.

In a few exceptional Monocotyledons (*e.g.* Dioscoreaceæ, Commelynaceæ) the growing-point of the primary stem is developed, not laterally, but apically, and the cotyledon is lateral. In some Dicotyledons (*e.g. Carum Bulbocastanum*, *Ranunculus Ficaria*) the embryo is *pseudo-monocotyledonous*; that is, only one cotyledon is developed though two are originally indicated.

In the Gymnosperms, the number of cotyledons varies from one of fifteen.

With regard to the histological differentiation of the embryo, the first step, after the division into octants, is the formation of periclinal walls marking off a superficial layer, which is the dermatogen (Figs. 286, 287); this differentiation proceeds from the anterior end, or apex, backwards towards the posterior end of the embryo. In those plants in which the root-end of the embryo is formed by a hypophysial cell contributed by the suspensor (Fig. 286 *B*, *h*), the dermatogen-layer is completed by the periclinal division of the hypophysial cell, the inner cell forming the periblem of the growing-point, the outer forming the dermatogen which undergoes further periclinal division to form the primitive root-cap. In the meantime, anticlinal and longitudinal walls have also been formed, so that the embryo, as it increases in size, consists of an increasing number of cells. The degree of histological differentiation attained varies widely: in the highest forms (Fig. 286 *D*) a cylinder of plerome is differentiated in the axis of the embryo, so that the three primary tissue-systems, dermatogen, periblem, and plerome, are clearly defined.

The degree of morphological differentiation attained by the embryo in its intra-seminal development also varies widely, as does also the size of the embryo. In the ripe seed of most Orchids and parasitic plants (*e.g.* Orobanche, Monotropa, etc.), the body of the embryo presents no differentiation into members. In most plants, the embryo, in the ripe seed, consists of the following members: (*a*) one, two, or several cotyledons; (*b*) a primary stem bearing the cotyledon or cotyledons, but not projecting beyond them, termed the *hypocotyl*, passing posteriorly into (*c*) the primary root or *radicle*. In some plants (*e.g.* Triticum and other Grasses, Phaseolus, Vicia, Amygdalus, etc.) the primary stem has elongated beyond the insertion of the cotyledon or cotyledons, and bears the rudiments of future foliage-leaves: this portion of the primary shoot is termed the *plumule* or *epicotyl*.

The size and texture of the cotyledons vary with the functions which they have to perform. When, as in exalbuminous seeds, such as peas and beans, the cotyledons are themselves the storehouses in which food is deposited for the nutrition of the embryo during its extra-seminal development, they are relatively large, thick, and fleshy; but when, as in albuminous seeds (*e.g.* Ricinus, Grasses, etc.), the food is stored in the endosperm, the cotyledons are absorbent organs and, though still relatively large, are not thick and fleshy.

In a few Phanerogams (*e.g.* Utricularia, which never developes any root, *Ruppia rostellata*, *Wolffia arrhiza*) no primary root is developed or even indicated.

The *extra-seminal development* of the embryo may be briefly stated as follows:—The first event is the elongation of the hypocotyl, with the result that the radicle passes, through the micropyle, out of the seed into the soil, where it becomes firmly attached: where (as in some Gymnosperms, Grasses, Tropæolum) the growing-point of the root is developed deep in the tissue of the embryo, the radicle, before it can escape from the seed, has to penetrate this more or less considerable mass of tissue which can be seen, on examining the germinated seed, as a collar, termed the *coleorhiza*, surrounding the base of the radicle. The other members then escape from the seed, the coat of which becomes more or less split. In those cases in which the growth of the hypocotyl is active, the cotyledons appear above the surface of the soil, that is, they are *epigean* (*e.g.* Cucurbita, Ricinus, Radish, Sunflower, Scarlet Runner, etc., most Gymnosperms), either leaving the seed-coat in the soil, or carrying it up to the surface. In those cases in which the growth of the hypocotyl is comparatively slight, the cotyledons do not reach the surface of the soil, that is, they are *hypogean* (*e.g.* *Vicia Faba*, Pea, Grasses, etc.): here it is the epicotyl (plumule) which grows rapidly, and is the first member to appear above ground. The part which first appears above ground, whether it be hypocotyl, epicotyl, or cotyledon, usually does so in the form of an arch, so that the apex is not exposed to injury whilst the member is forcing its way up through the soil.

Epigean cotyledons become green in colour, and in many cases (*e.g.* Sunflower, Radish) assume the appearance, and discharge the functions, of foliage-leaves; but they do not ever precisely resemble, either in size or form, the true foliage-leaves of the plant to which they belong.

Vegetative Propagation is common among Phanerogams, by means of bulbs (*e.g.* Lily, Onion, and many other Monocotyledons), tubers (Potato), tuberous roots (Dahlia), etc.

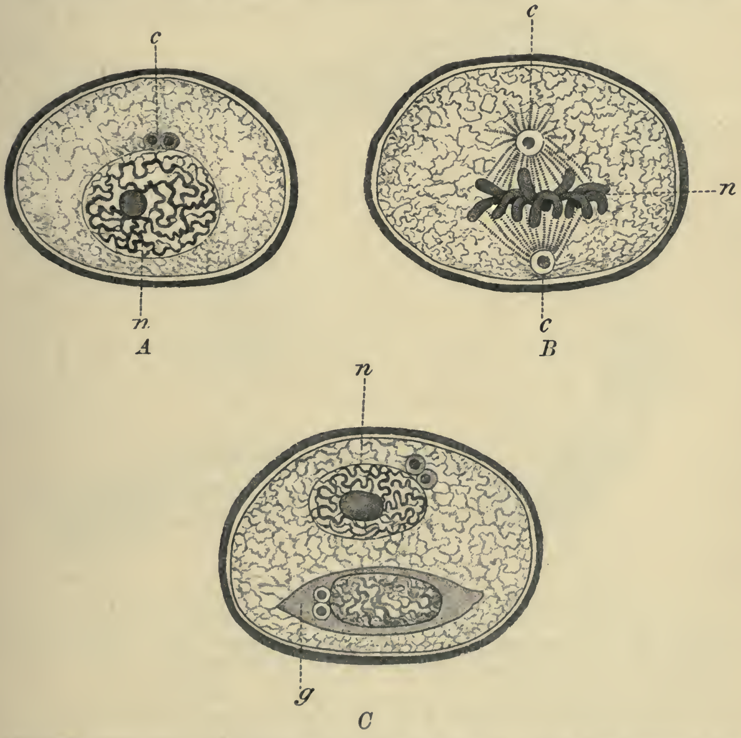

FIG. 288.—Germination of pollen-grain of *Lilium Martagon* (×750: after Guignard). *A* Young pollen-grain: *c* centrospheres; *n* resting nucleus. *B* Commencement of germination: *n* the dividing nucleus; *c* centrospheres. *C* Cell-formation has taken place, resulting in the formation of the generative cell *g*; *n* nucleus of remainder of pollen-grain (*i.e.* vegetative cell).

B. THE GAMETOPHYTE. As all Phanerogams are heterosporous, the sexual generation is represented by two individuals, a male and a female, developed respectively from the microspore and the macrospore.

The *Male Prothallium* is, in all cases, filamentous and relatively small, consisting of but few cells. The first indication of its development is the division of the nucleus of the microspore, which may take place even before the microspore escapes from the microsporangium, and this is followed by cell-formation. In the Angiosperms (Fig. 288) the cell-formation is simple, consisting in the aggregation of protoplasm round one of the two nuclei, without any formation of cell-wall, so that a small primordial cell, the *generative* cell, is formed, floating freely in the protoplasm of the microspore which, with the other nucleus, constitutes the *vegetative* cell. In the Gymnosperms the process is rather more complicated. In the simplest case (*e.g.* the Yew, Fig 289) the microspore divides into two cells, separated by a cell-wall; of these the one, the antheridial cell, undergoes division into two, a stalk-cell (*st*) and a generative cell (*an*); whilst the other remains as an undivided vegetative cell. In some cases,

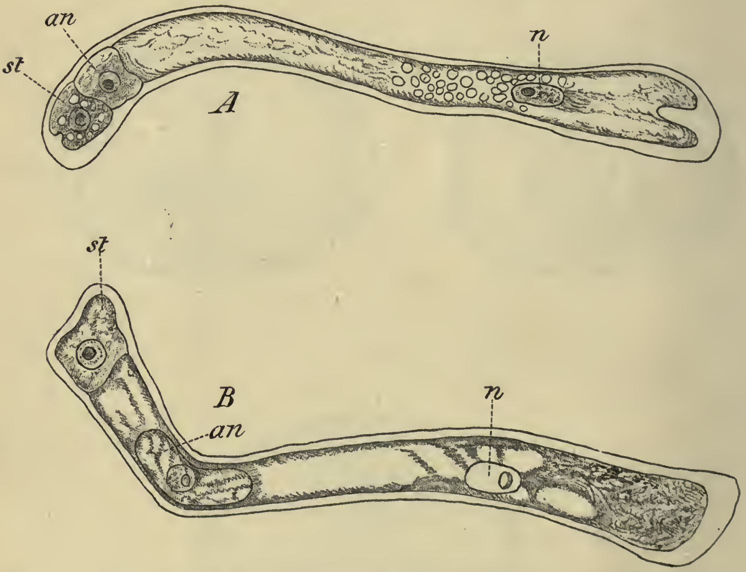

FIG. 289.—Development of male prothallium from the pollen-grain of the Yew: *A* early stage. *B* Later stage: *st* stalk-cell; *an* antheridial cell; *n* nucleus of the large vegetative cell which has grown out into the pollen-tube. In *B* the generative cell is travelling down the pollen-tube as a preliminary to fertilisation. (× 350: after Belajeff.)

however (*e.g.* Larch, Ginkgo, Fir, Ephedra), generally three cells are successively cut off by parallel septa (Fig. 290): of these, the two first formed are merely vegetative prothallial cells, and undergo disorganisation, whilst the last is the antheridial cell, and undergoes division into a generative cell and a stalk-cell. In some cases (Ginkgo, Ephedra, Cycads) the second prothallial cell persists; and it appears that in the Gnetaceæ the antheridial cell does not divide to form a stalk-cell but is actually the generative cell.

In both Angiosperms and Gymnosperms, the pollen-tube is formed by the outgrowth of the large vegetative cell: in both cases the generative cell (after being set free when necessary) enters the pollen-tube, together with the vegetative nucleus, and, in Gymnosperms, with the nucleus of the stalk-cell; the vegetative nucleus becomes disorganised (Fig. 289 *B*, *n*), whilst the generative cell undergoes division into two; either into two equal generative cells, as is generally the case, or into two unequal cells only one of which is generative (*e.g.* Taxus). More than one pollen-tube may be developed from the microspore (Fig. 283).

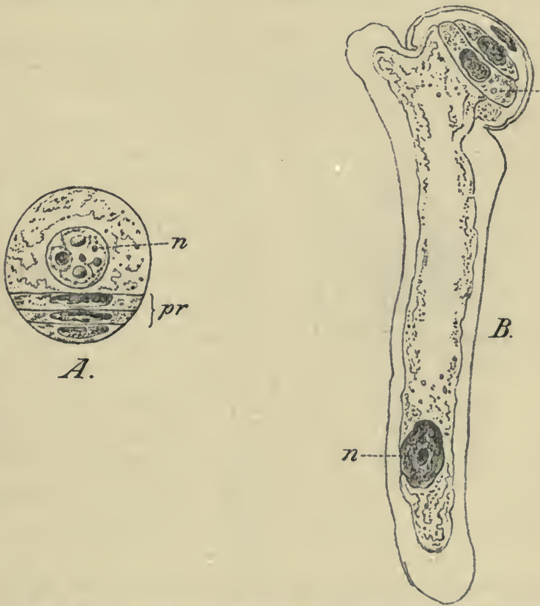

FIG. 290.—Development of the male prothallium of *Ginkgo biloba*. *A* Pollen-grain in which cell-division is proceeding whilst still in the pollen-sac; *n* nucleus: *pr* three prothallial cells, the innermost of which is the antheridial cell. *B* Older pollen-grain developing a pollen-tube; *pr* prothallial cells; *n* nucleus of pollen-tube. (× 540: after Strasburger.)

Thus the male individual in the Phanerogams is a prothallium consisting of but few cells, and the antheridium is at most two-celled: the generative cell represents a spermatozoid-mother-cell, the protoplasm of which is not, however, differentiated into a spermatozoid, but simply constitutes a male cell.

The *male cell* is a small nucleated primordial cell in the pollen-tube, and is either the original generative cell itself, or a product of its division. It is eventually extruded through the apex of the pollen-tube.

The *Female Prothallium* is developed in the interior of the macrospore (embryo-sac) in a similar manner to that of the heterosporous Pteridophyta: but, in the Phanerogams it does not at any period project from the macrospore as it does in the Pteridophyta, though this occurs exceptionally in the Cycadaceæ among Gymnosperms, and in Avicennia among Angiosperms.

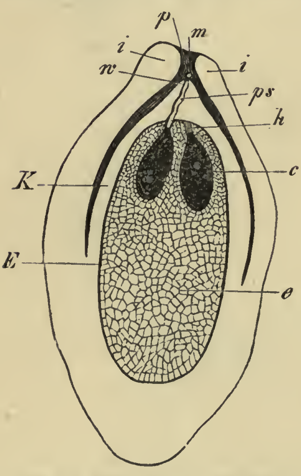

Fig. 291.—The female prothallium of Gymnosperms, shown in a longitudinal section of the ovule (× about 15; diagrammatic): *ii* integument; *m* micropyle. *K* Nucellus (macrosporangium). *E* Embryo-sac (macrospore); *e* female prothallium (endosperm), in which are situated, towards the micropyle, two archegonia, *c*, with neck *h*; *ps* pollen-tube entering the neck of the left archegonium; *p* pollen-grain seated on the apex of the nucellus.

The development of the prothallium (or endosperm) is simple in the Gymnosperms. The nucleus of the macrospore divides; repeated nuclear division takes place, until a large number of nuclei are formed which lie in the protoplasm round the wall of the macrospore; between these nuclei cell-walls are developed, so that a cellular tissue is produced, the cells of which grow and multiply by division until the cavity of the macrospore is entirely filled with this tissue which constitutes the prothallium. In Gnetum, however, the development of the prothallium is not completed until fertilisation has taken place.

In the Angiosperms the development of the prothallium is more complicated in that it generally takes place in two stages, the one preceding, the other following, fertilisation. The nucleus of the macrospore divides into two: of these the one travels to the micropylar pole, the other to the chalazal pole, of the macrospore; each nucleus then divides, and each of the four so formed divides again, so that eight nuclei are formed, four at the micropylar, and four at the chalazal pole of the macrospore; one nucleus is then conveyed from each pole toward the centre of the macrospore, where the two nuclei meet and fuse into one which is termed the *definitive nucleus* of the macrospore or embryo-sac. Three nuclei now lie at each pole, and around these aggregation of protoplasm takes place, so that cells are formed: those at the chalazal pole soon acquire a cell-wall, and are termed *antipodal cells*: those at the micropylar end do not form any cell-wall; one of them is the female reproductive cell or oosphere, the other two are sterile (though in rare cases they are fertile), and are termed the *synergidæ*, the three together constituting the *egg-apparatus*. This is the extent to which the development of the female prothallium takes place previously to fertilisation. In most Angiosperms the structure of the prothallium is completed by the formation, after fertilisation has taken place, of additional cellular tissue: this process is initiated by the division of the definitive nucleus of the macrospore, nuclear division is repeated, cell-formation takes place, in the manner described above for the Gymnosperms, and the macrospore becomes more or less completely filled with cellular tissue, commonly termed *endosperm*.

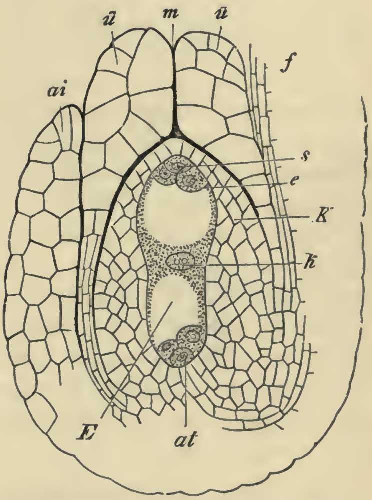

Fig. 292.—The female prothallium of Angiosperms, shown in a longitudinal section of the ovule (× 70): *ai* outer, *ii* inner, integument; *m* micropyle; *f* funicle. *K* Macrosporangium (nucellus). *E* Macrospore (embryo-sac). *k* Definitive nucleus of the embryo-sac. The female prothallium consists of the egg-apparatus at the micropylar end of the macrospore, and of the group of antipodal cells *at* at the chalazal end. The egg-apparatus consists of two synergidæ *s*, and an oosphere *e*.

In a number of dicotyledonous plants (*e.g.* Loranthaceæ, Orobanchaceæ, Labiatæ, Campanulaceæ) where the embryo-sac is long and narrow, the endosperm is developed by cell-division: the embryo-sac is divided by two or more transverse septa and longitudinal divisions follow. And even when the development of the endosperm begins with free cell-formation, its further development is effected by the growth and division of the first-formed cells.

The degree of development attained by the endosperm in Angiosperms is various. Whilst, as a rule, it completely fills the embryo-sac, leaving room, however, for the embryo, in some cases it occupies but a portion of the embryo-sac, as in the Coco-nut, where it forms a thick parietal layer; or, as in Nymphæa, Nuphar, Anthurium, Viscum, Lathræa, Thesium, Rhinanthus, etc., where the development of endosperm is confined to the upper half of the embryo-sac. In some cases the endosperm is rudimentary, being represented merely by a number of nuclei, as in Tropæolum, Trapa, Naiadaceæ, Alismaceæ, Orchidaceæ; and in Canna even this rudimentary development is wanting.

The antipodal cells do not, as a rule, undergo any further development, but in some cases (*e.g.* some Graminaceæ) they have been observed to divide and give rise to a considerable mass of cells.

The *female organ* is essentially an archegonium. In most Gymnosperms it is actually an archegonium, like that of the Pteridophyta; it is developed from a single superficial cell of the prothallium at the micropylar end, and has a neck, containing a canal-cell, leading to a ventral cavity in which lies the *female cell* or *oosphere*; but in Welwitschia the archegonium is reduced to a single cell with a cell-wall; and in Gnetum to a single cell without a cell-wall, the oosphere. In the Angiosperms the female organ resembles that of Gnetum, in that it is reduced to a single naked cell: the three cells constituting the egg-apparatus represent each an archegonium reduced to a single cell; but in one only is this cell a true fertile oosphere, the other two (the synergidæ) being sterile as a rule.

In a few plants the egg-apparatus consists of but two cells (the rule in *Santalum album*; occasionally in *Ornithogalum nutans*, Sinningia, Gomphrena, some Orchids such as *Orchis latifolia*, *Cypripedium Calceolus*, *Gymnadenia Conopsea*, some Mimoseæ): it would appear, that, in such a case, there has been but one nuclear division in the micropylar end of the embryo-sac. Both the cells are susceptible of fertilisation, and are therefore both to be regarded as oospheres.

In some plants (Crocus, Gladiolus, Torenia Fig. 285, Santalum) the synergidæ become elongated, and penetrate the wall of the embryo-sac; their projecting ends are longitudinally striated and are covered with a coat of cellulose: these structures are sometimes spoken of as the *filiform apparatus*.

In Casuarina, the cells of the egg-apparatus (when fertile) are surrounded by cell-walls (like the oosphere of Welwitschia): no antipodal cells are developed.

Pollination. In view of the fact that the female cell (oosphere), and the prothallium bearing it, remain (as a rule) permanently enclosed in the macrospore, and that the macrospore remains enclosed in the indehiscent macrosporangium, it is clear that the process of fertilisation can only be effected when the microspore germinates in immediate proximity to the macrosporangium.

The bringing of the microspore into such close relation is what is termed *pollination.* When the pollen of any one flower is brought into relation with the macrosporangium of the same flower, the case is one of *self-pollination*; when the pollen of any one flower is brought into relation with the macrosporangium of another flower (whether on the same plant, or on another plant of the same species), the case is one of *cross-pollination.*

The microspores when so brought are placed under conditions of moisture and nutrition favourable to their germination. In Gymnosperms, where there is no ovary and no stigma, the microspore is brought into direct contact with the micropyle of the macrosporangium. In the Angiosperms, where there is an ovary and a stigma, the microspores cannot come into direct contact with the macrosporangium; they fall upon the stigma and germinate on its moist surface; the pollen-tubes then grow down into the ovary, down the style, if there is one, and finally enter the ovules (see Fig. 280).

In certain cases flowers, of course ambisporangiate, are so modified as to ensure self-pollination: instances of this are afforded by species of Viola, *Lamium amplexicaule*, *Oxalis Acetosella*, and others, where the plant (in addition to the ordinary flowers) bears inconspicuous flowers which do not open, and in which self-fertilisation is perfectly effected by the pollen; these peculiar flowers are said to be *cleistogamous.*

In the great majority of Phanerogams, however, cross-pollination is the rule. In the case of monosporangiate flowers (*e.g.* Gymnosperms) it is clear that pollen must be conveyed from a staminate to a carpellary flower. It is also known that in a great number of ambisporangiate flowers, pollination is effected by the transfer of pollen from one flower to another: in some of these cases it has been demonstrated that it is only the pollen of another flower which can effect fertilisation; in other cases, that the pollen of the same flower, though not absolutely useless, has less fertilising power than that of another flower; and in yet other cases, that though the pollen of the flower itself has sufficient fertilising effect, yet the progeny is less vigorous than when pollen is supplied from another flower.

The conveyance of pollen from one flower to another is effected, in the case of a number of plants with inconspicuous flowers (*e.g.* Gymnosperms, Grasses, many Dicotyledonous Forest-trees), by the agency of the wind, when they are said to be *anemophilous*; but in the case of flowers which are conspicuous by their size, colour, perfume, or by their secretion of honey, the conveyance is effected by the insects which are attracted to visit the flowers; such flowers are said to be *entomophilous*.

In those ambisporangiate flowers to which cross-fertilisation is indispensable, or at least important, the most various contrivances are exhibited for the purpose of hindering or limiting self-pollination on the one hand, and, on the other, of facilitating cross-pollination; or finally, in default of cross-pollination, of ensuring ultimate self-pollination, this last, of course, only in those cases in which the pollen of the flower itself is capable of fertilising it; for it is evident that self-pollination, even if not very advantageous, is at any rate of some use to the plant.

Among the contrivances for the prevention of self-pollination, one of the simplest is the arrangement of the anthers and stigma in such positions that the pollen cannot possibly reach the stigma of the same flower, *e.g.* Aristolochia (Fig. 293): or secondly, the abortion of all the microsporangia in some flowers and of all the macrosporangia in others; in such flowers the organs in question are present, but they are not functional. This is an approach to the diclinous condition; it occurs in the Tiger-Lily, in which the anthers are commonly abortive in some flowers and the ovaries in others. Thirdly, *dichogamy* frequently occurs, that is, that the stigmata and stamens attain their functional activity at different times: flowers in which this occurs are either *protandrous*, that is, the anthers are first developed and have already shed their pollen when the stigma of the same flower is capable of receiving it; or they are *protogynous*, that is, the stigma is fully developed before the anthers of the same flower are ready to shed their pollen: in the latter case self-pollination is obviously only excluded if the stigma is withered before the pollen is shed; there are, however, protogynous flowers in which the stigma remains fresh for a long time and which may be pollinated by their own pollen. As examples of protandrous flowers, those of the Umbelliferæ, and most of the Compositæ, Lobeliaceæ, and Campanulaceæ may be mentioned; and of protogynous flowers, Aristolochia, Arum, *Scrophularia nodosa*, and some species of Plantago, but this condition is less common than the preceding.

Among the contrivances which lead to the cross-pollination of flowers by the agency of insects, the means of tempting insects to visit the flowers, such as bright colours, odours, and the secretion of honey, must be first mentioned. The peculiar marking of the flower serves in many cases the purpose of guiding insects to the nectary. The form of the flower, the situation of the honey, the position of the stamens, and their relation to the other parts of the flower, particularly to the stigma, the relative development in point of time of the different parts, all these circumstances combine and co-operate to secure cross-pollination, and sometimes to allow of the visits of particular insects only, as, for instance, of butterflies with long probosces, though there are also cases in which the insects must occasionally convey the pollen to the stigma of the same flower. A simple arrangement of this kind known as *heterostylism* or *dimorphism*, and which occurs in species of Primula, Pulmonaria, Linum, Polygonum, etc., may be mentioned here. These plants have two forms of flowers; in one form the stamens are short and the style much longer, so that the stigma projects above the anthers; in the other form, on the contrary, the anthers are on long filaments above the stigma; they are both so constructed that the anthers of one form stand on the same level as the stigma of the other. From the position of the nectary, and the form of the rest of the flower, an insect visiting it is obliged to take up the same position at each visit; consequently after it has visited a flower of the one form, when it visits a flower of the other form, it touches the stigma of the latter with the same part of its body with which in the first flower it brushed the anthers, and thus the pollen which it carried away with it from the anthers of the one flower is transferred to the stigma of the other. Observations made by artificially transporting the pollen have shown that fertilisation is most complete when the pollen of stamens of a certain length is conveyed to the stigma of a style of the same length. The same is the case with *trimorphic* plants, *e.g.* Oxalis, *Lythrum Salicaria*: in these, three forms of flowers occur with three different lengths of styles and stamens.

As examples of more complicated contrivances for the purpose of securing cross-pollination, Aristolochia and Epipactis may be described.

The flower of *Aristolochia Clematitis* (Fig. 293) is protogynous; insects can penetrate without difficulty down the tube of the perianth, which is furnished on its internal surface with hairs which point downwards, and they thus convey the pollen they have brought with them from other flowers, to the stigma; the hairs, however, prevent their return. When the pollen has reached the stigma, its lobes (Fig. 293 *A* and *B n*) spring upwards, and thus the anthers, which now begin to open, are made accessible to the insects; these, in their efforts to escape (Fig. 293 *i*), creep round the anthers and some of the pollen adheres to them; by this time the hairs in the tube have withered, and the insect escapes, dusted over with pollen which, in spite of experience, it proceeds to convey in like manner to another flower. Those flowers which are ready for pollination have an erect position, and the tube of the perianth is open above so that the insect can readily enter; after pollination the peduncle bends downwards and the tube is closed by the broad lobe of the perianth, so that it is impossible for insects to enter flowers which have been fertilised.

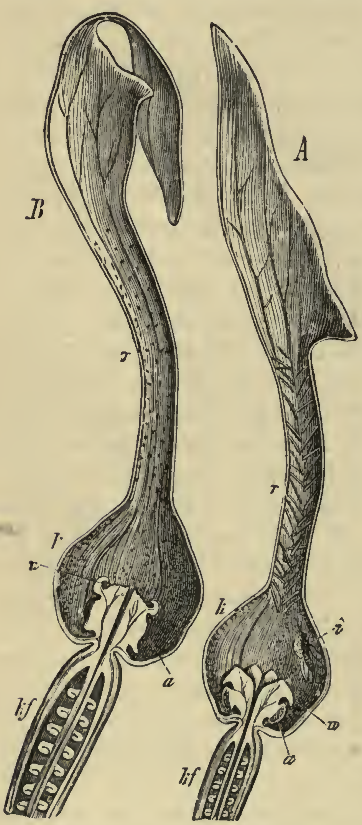

FIG. 293.—Flower of Aristolochia. *A* Before, and *B* after fertilisation; *r* the tube of the perianth; *k* the cavity below; *n* stigma; *a* anthers; *i* an insect; *kf* ovary. (After Sachs.)

In the flower of Epipactis (one of the Orchidaceæ), the anther is situated above the stigma and does not shed its pollen in isolated grains; but when a certain portion of the stigma (the abortive anterior lobe), known as the *rostellum* (Fig. 294 *h*), is touched, the two pollinia, together with a mass of sticky substance (*retinaculum*) derived from the rostellum, are removed from the pollen-sacs, adhering to the foreign body (Fig. 294 *F*, *h*). The insect creeps into the flower to obtain the honey which is secreted in the cavity of one of the leaves of the perianth, the *labellum* (Fig. 294 *l*); as it withdraws from the flower, it carries away the pollinia on its head, and on entering the next flower, deposits them upon the stigma.

In the course of frequent cross-pollination it is inevitable that the pollen of other species of plants should be applied to the stigma; but while the pollen of plants of widely different species is wholly without effect, that of nearly allied species, particularly those belonging to the same genus in certain groups, has a fertilising effect; the result of cross-fertilisation between species is *hybridisation*, that is, the development of a plant which combines the characters of both parent-species to a certain extent, and which is known as a *bastard* or *hybrid*. Hybrids are for the most part sterile among themselves, but are often fertile when crossed again with a plant of either of the parent-species or of some allied species. While hybrids are produced with great ease in certain genera, as Salix and Cirsium, in others the artificial production of hybrids has never yet been found possible even between very closely allied species, as the Apple and Pear.

Fertilisation. As in other plants, so here, the process of fertilisation consists in the fusion of the male and female reproductive cells. The way in which it takes place in Phanerogams is briefly as follows:—The pollen-tube makes its way to the female organ, entering the neck of the archegonium in the Gymnosperms, and coming into close relation with the egg-apparatus in the Angiosperms. The apex of the wall of the pollen-tube is at this time mucilaginous: a small nucleated mass of protoplasm, the male cell (see p. 450), is forced out through the mucilaginous membrane, into the oosphere; the nucleus of the male cell (*male pronucleus*) and that of the female

FIG. 294.—*Epipactis latifolia*. *A* Longitudinal section through a flower-bud. *B* Open flower after removal of the perianth, with the exception of the labellum, *l*. *C* The reproductive organs, after the removal of the perianth, seen from below and in front. *D* as *B*: the point of a lead-pencil (*b*) is inserted after the manner of the proboscis of an insect. *E* and *F* The lead-pencil with the pollinia attached; *f K* ovary; *l* labellum, its sac-like depression serving as a nectary; *n* the broad stigma; *cn* the connective of the single fertile anther; *p* pollinia; *h* the rostellum; *x x* the two lateral staminodes; *i* place where the labellum has been cut off; *s* the gynostemium. (After Sachs.)

cell (*female pronucleus*) approach each other and fuse into one, the two protoplasms likewise fusing. Fertilisation is now complete; in consequence, the oosphere surrounds itself with a cell-wall, becoming the oospore, and begins to develope into the embryo-sporophyte. Further details are given in the sections on Gymnosperms and Angiosperms respectively.

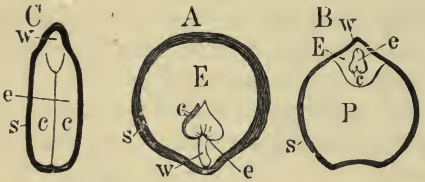

Fig. 295.—Sections of ripe seed. *A Nux vomica*, showing *E* endosperm. *B* Piper, showing both endosperm *E*, and perisperm *P*. *C* Almond, devoid of endosperm; *s* the testa; *e* embryo; *w* its radicle; *c c* its cotyledons.

The Results of Fertilisation. The most direct result of fertilisation is the development of the embryo from the fertilised oosphere, a process which involves the conversion of the ovule into the seed. But the effect of fertilisation is not limited to this: other parts of the flower are affected in such a way that they undergo marked changes in structure, accompanied by considerable increase in size, the product being the structure known as the *fruit* (p. 88). In some cases the carpels only are affected, becoming either fleshy and succulent (*e.g.* Plum), or dry and hard (*e.g.* Poppy); in others, the floral axis becomes fleshy (*e.g.* Strawberry); in others again the perianth-leaves also (*e.g.* Mulberry). It is convenient to regard as *true fruits* only those which are developed from the gynæceum alone; and as *false fruits*, or *pseudocarps*, those in the formation of which other parts of the flower or of the inflorescence take part.

The seed (p. 88) is produced from the ovule, as a consequence of the fertilisation of the female cell contained within the ovule: its characteristic feature is that it contains an embryo. The seed (Fig. 295) may contain little or nothing but the embryo, in which case it is said to be *exalbuminous* (*e.g.* Pea, Bean, Sunflower, Almond, Oak): or it may contain, in addition to a small embryo, a considerable portion of the female prothallium (endosperm), when it is termed *albuminous* (*e.g.* Grasses and most Monocotyledons, Ranunculaceæ): in a few rare cases the albuminous seed contains, in addition to the embryo and endosperm, some of the nucellar tissue of the macrosporangium which is termed *perisperm* (*e.g.* Piperaceæ, Nymphæaceæ, Zingiberaceæ): in Canna, Chenopodiaceæ, Amarantaceæ, Phytolaccaceæ, and Nyctaginaceæ, there is perisperm but no endosperm in the ripe seed, though it has been ascertained in some cases that endosperm is originally formed.

A formation of endosperm takes place in nearly all seeds, even exalbuminous seeds, but in these latter it is more or less disorganised and absorbed by the growing embryo, so that little or none remains in the ripe seed.

Whether the seed be albuminous or exalbuminous, it contains (except in some parasitic or saprophytic plants, such as Orchids, etc.) a supply of organic substances for the nutrition of the embryo during its extra-seminal period of development. These substances may be mainly stored in the cells of the cotyledons, as in exalbuminous seeds; or in the cells of the endosperm, or in the cells of the perisperm, when present, as in albuminous seeds. The substances are nitrogenous and non-nitrogenous. The nitrogenous substances are proteids, deposited in the solid form as aleuron (see p. 112), and are present in all seeds. The non-nitrogenous substances are starch, in the form of starch-grains (see p. 109), in starchy seeds (*e.g.* Peas, Beans, Cereals, etc.); or fat, in the form of oil-drops (see p. 111), in oily seeds (*e.g.* Linseed, Rape, Castor-Oil seed, etc.).

The seed is generally enclosed in a single integument, the *testa*, derived from the outer integument of the ovule, the inner integument of the ovule having been absorbed; sometimes, however, the seed has two integuments derived from those of the ovule, an outer *testa*, and an inner *endopleura* (*e.g.* Euphorbiaceæ, Rosaceæ): in others again neither of the ovular integuments persists into the seed, in which case the wall of the embryo-sac is in direct contact with the wall of the ovary.

In a few cases additional integuments or appendages are developed in connexion with the seed, such new growths being designated by the general term *aril.* The aril may be developed from either the funicle or the hilum; or from the micropyle, when it is distinguished as an *arillode.* Good examples of a funicular aril, which grows up round the seed like an additional integument, are afforded by the Yew, Water-Lily (Nymphæa), Passion-Flower. The Willow has a funicular aril in the form of a tuft of woolly hairs. The most striking example of a membranous micropylar aril is the Spindle-tree (Euonymus): in Euphorbia and Polygala the micropylar aril is a small mass of tissue, and in Asclepias it is a tuft of hairs. Other excrescences, not especially connected with either the hilum or the micropyle (sometimes distinguished as *caruncles* or *strophioles*), occur in certain plants: thus in the Violet and the Celandine (Chelidonium) an elevated ridge marks the course of the raphe, and in the Willow-herb (Epilobium) a tuft of hairs springs from the chalaza.

The most important point to be considered is, however, that of the structural conditions which determine the production of a seed in the Phanerogams, the feature which sharply defines this group of plants from all others. The structural conditions are briefly as follows:—the macrospore (embryo-sac) is not set free from the macrosporangium (ovule), as is the case in the heterosporous Pteridophyta; nor does the macrosporangium itself separate from the plant producing it until it has ripened into the seed: this being so, the macrospore germinates inside the macrosporangium, producing there the female prothallium with its reproductive organs: fertilisation of the oosphere, as also the development of the embryo from the oospore, takes place inside the macrospore; and thus the seed is formed. If the macrospore were set free from the macrosporangium, no seed would be formed; but in that case the condition of things would be that which actually exists in the higher heterosporous Pteridophyta, such as Selaginella.

Some seeds can germinate as soon as they are shed: but, for the most part, they only do so after a period of quiescence, though they may lose their germinating power if this period be too prolonged.

The Dissemination of the Seed. Fruits are either *dehiscent*, so that the seeds escape, or are *indehiscent*: in the former case the seeds, and in the latter case the fruits, present various adaptations for ensuring their dispersion. The most conspicuous are those which ensure dispersion by the wind: of this nature are the wing-like appendages of the fruit in the Maple, Ash, Ailanthus, Elm, etc.; and of the seed of Pinus, Tecoma, Catalpa, etc.: also the hairy appendages of fruits (*e.g.* the pappus of Compositæ, the feathery style of Clematis, etc.), and of seeds (*e.g.* on those of Gossypium the Cotton-plant, Willow, Poplar, Asclepias, etc.). Other adaptations ensure dispersion by animals; such are the hooks on fruits (forming burrs), as in various Boraginaceæ, Compositæ, Galium, etc.: the succulence and agreeable taste of many indehiscent fruits also promotes the dispersion of the seeds, the fruits being eaten by animals and the seed being protected from digestion by hard protective tissue either in the fruit (endocarp) or in the seed-coat (testa). In some cases (*e.g. Ecballium*

Elaterium, the Squirting Cucumber; *Impatiens noli-me-tangere; Oxalis Acetosella; Hura crepitans*) the fruit dehisces suddenly, ejecting and scattering the seeds with considerable force. Some fruits, provided with a long appendage (awn), bore their way into the soil (*e.g. Stipa pennata*, Erodium).

The Life-History of the Phanerogams is essentially similar to that of the heterosporous Pteridophyta, though, on account of the structural peculiarities which bring about the formation of a seed, it is not quite so easy to trace. The sporophyte, or asexual generation, is represented by the plant itself, bearing macro- and micro-sporangia and macro- and micro-spores. The gametophyte, or sexual generation, is represented by the male and female prothallia developed respectively from the microspore and the macrospore. Thus there is a definite and regular alternation of generations, since the male and female prothallia can only be developed from the spores of the sporophyte; and, on the other hand, the sporophyte can only be developed from the immediate product of fertilisation, the oospore.

The gametophyte is here very much reduced, even more so than in the highest heterosporous Pteridophyta, especially as regards the female individual. In the Phanerogams, in consequence of the indehiscence of the macrosporangium and of its remaining attached to the plant producing it, the macrospore germinates whilst still in organic connexion with the sporophyte, with the remarkable consequence that the female individual (or prothallium) is actually an appendage of the sporophyte, and seems to be so much a part of it that its true morphological significance is easily overlooked.

The life-history of these plants is made clear by a morphological consideration, as indicated in the following table, of the structure of the seed:—

Seed-coats . . . }
Perisperm (if present) } = macrosporangium of parent-sporophyte.
Endosperm . . . = gametophyte: female prothallium.
Embryo . . . = young sporophyte.

When a plant perishes after once producing flowers and seeds, it is said to be *monocarpous*. In rare cases (*e.g. Agave americana*) several or even many years elapse before the plant blooms: more common are *annual* plants (indicated by the sign ⊙), *i.e.* such as complete the whole course of their development in a single year, as the Wheat; and *biennials*, which do not blossom until the second year of their life, when they perish, as the Turnip, Carrot, Beetroot, etc. By *polycarpous* plants are meant such as produce flowers and fruit year after year; such are trees and shrubs, as also many herbaceous plants which have underground rhizomes, tubers, etc.

The group of the Phanerogams falls into two natural divisions; the one containing but a single class; the other, two classes.

A. GYMNOSPERMÆ.

Sporophytic Characters. The ovule is not enclosed in an ovary, nor is there any style or stigma: in pollination, the pollen-grain enters the micropyle and comes into direct contact with the nucellus: the flowers are never ambisporangiate, and are generally without a perianth: there are no companion-cells in the phloem, and the secondary wood does not (except Gnetaceæ) contain true vessels.

Gametophytic Characters. The female prothallium is completely formed before fertilisation: the female organ is generally a well-developed archegonium.

Class I.—Gymnospermæ.

B. ANGIOSPERMÆ.

Sporophytic Characters. The ovule is enclosed in an ovary, and there is always a stigma: the pollen-grain does not come into direct relation with the ovule, but falls upon the stigma and germinates there: the flowers are commonly ambisporangiate and possess a perianth: there are companion-cells in the phloem, and the secondary wood generally includes true vessels.

Gametophytic Characters. The female prothallium is only partly formed before fertilisation: the female organ is a reduced unicellular archegonium.

Class I.—Monocotyledones. The embryo has but one cotyledon: the ripe seed is usually albuminous.

Class II.—Dicotyledones. The embryo has two opposite cotyledons: the ripe seed is frequently exalbuminous.

DIVISION A.

CLASS I.—GYMNOSPERMÆ.

The plants of this class are all perennial trees and shrubs, for the most part evergreen: they are classified into the three natural orders, Cycadaceæ, Coniferæ, and Gnetaceæ.

THE SPOROPHYTE.

General Morphology of the Vegetative Organs. The body is distinctly differentiated into stem, leaf, and root.

The *Stem* grows above ground, usually erect, but climbs in several species of Gnetum: it is woody, and is generally branched monopodially: the symmetry of the main stem is radial, whilst that of the branches is frequently bilateral, either isobilateral (*e.g.* Thuja, phylloclades of Phyllocladus) or dorsiventral (*e.g. Thujopsis dolabrata*, *Abies Nordmanniana* and *concolor*, Taxus, Torreya, and many other Coniferæ in which the branches are horizontal). The branches in many Coniferæ (*e.g.* Pinus, Sciadopitys, Phyllocladus, Larix, Taxodium, Cedrus, Ginkgo) are dimorphous, being either long shoots or dwarf-shoots (see p. 39): in Phyllocladus the dwarf-shoots are developed into phylloclades; in the other forms the dwarf-shoots all bear foliage-leaves and fall off, sooner or later, with the leaves which they bear: in Pinus and Sciadopitys the dwarf-shoots alone bear foliage-leaves, whilst in the other genera the long shoots bear foliage-leaves as well.

The *Leaves* are either foliage-leaves or scale-leaves. The foliage-leaves are either small and numerous, as in the Coniferæ; or large and few, as in the Cycadaceæ, and as in Welwitschia where there are only two foliage-leaves: they are branched only in the Cycadaceæ: they are sessile in the Coniferæ and in Welwitschia: their growth is basal: their form varies considerably, one of the most peculiar forms being that characteristic of certain Coniferæ (Abietineæ) where the leaf is needle-like (acicular) and either flattened or prismatic and angular. Larix, Ginkgo, *Taxodium distichum*, and Glyptostrobus, are the only forms in which the leaves fall annually; in the others the leaves persist for two to ten years, or, as in Welwitschia, throughout the life of the plant. Foliage-leaves are absent in Phyllocladus and generally in Ephedra. A certain amount of heterophylly is observable in some cases: thus the leaves of the shoots bearing flowers sometimes differ from those of the vegetative shoots, as in *Dacrydium cupressinum*, where the leaves of the fertile shoots are scale-like and radially arranged, whilst those on the vegetative shoots are linear and are arranged in two lateral rows; or as in *Sequoia gigantea* where the leaves of the fertile shoots are shorter, broader, and more closely arranged than of the vegetative shoots: or the younger leaves may differ from the older, as, for instance, in certain Cupressineæ with scale-like foliage-leaves, where the first foliage-leaves of the young stem are acicular (Thuja), or where some of the branches bear acicular leaves (Juniperus): or in these same Cupressineæ (*e.g.* Thuja) the leaves borne on the flanks of the shoot differ in shape from those on the upper and lower surfaces, the latter being further distinguished by having each a resin-receptacle (see Fig. 306, p. 486).

Scale-leaves, destitute of chlorophyll, occur in nearly all the Cycadaceæ, in most Conifers (absent in most Cupressineæ and Araucarieæ) and in Ephedra (Gnetaceæ). In the Cycadaceæ the scale-leaves are present in great number, completely covering the surface of the stem, and are developed at the growing-point alternately with the foliage-leaves, but in much greater numbers: in Pinus, Phyllocladus, and Sciadopitys, the scale-leaves are the only leaves borne by the long shoots; in Phyllocladus and Ephedra they are the only vegetative leaves.

The *Primary Root* always persists as a tap-root.

General Histology. The *Stem.* The growing-point of the stem generally described as presenting in the Abietineæ a well-marked differentiation into dermatogen, periblem and plerome, whilst in the other Coniferæ the distinction between periblem and plerome is less clear, and in Ephedra even the distinction between dermatogen and periblem is not definite; it has been asserted from time to time, though without absolute demonstration, that, in the Cycadaceæ, the Coniferæ, and in Gnetum and Ephedra among the Gnetaceæ, there is an apical cell, either three-sided or four-sided, in the growing-point.

The stem is monostelic: the stele is surrounded by a pericycle which may be simply parenchymatous (*e.g.* Pinus) or consist of thick-walled fibres (*e.g.* Taxus): the primary vascular bundles are collateral, are open, and have the usual general structure; they are generally arranged in a single circle round the pith, but in Cycas there is a system of cauline bundles in the cortex, in Encephalartos there is a similar system in the pith, and in Welwitschia there are apparently both a cortical and a medullary system. Secondary growth in thickness takes place as a rule by means of a normal cambium-ring; but in some cases the activity of the normal cambium is short-lived, and a new merismatic layer is developed in the pericycle; thus in Cycas, Encephalartos, and species of Gnetum, the merismatic layer resembles the true cambium in that it forms wood internally and bast externally, and in these plants successive merismatic layers are formed; in Welwitschia the merismatic layer forms vascular bundles and ground-tissue internally, and cortex externally, and persists throughout the life of the plant. In the Cycadaceæ and Coniferæ, the secondary wood consists exclusively of tracheides with rounded or elongated bordered pits (scalariform tracheides) and of parenchymatous medullary rays, but true vessels are formed in the Gnetaceæ; the secondary bast has generally the normal structure, but in some cases (Abietineæ) it has no bast-fibres.

The *Foliage-leaf* is characterised by its well-developed epidermis the cells of which are fibrous (Pinus, Torreya): the stomata are always depressed below the surface, and are borne usually on the under surface only, when the leaf is flat (*e.g.* Cunninghamia, Abies, Taxus, Ginkgo, etc.), or on both sides (some Araucarias, Podocarpus), or on the upper side only (Juniperus), but on all sides when the leaf is acicular (*e.g.* Pinus, Picea, etc.): the epidermis is supported by a hypodermal layer of fibrous sclerenchymatous cells; when the leaf is flat, the mesophyll is more or less clearly differentiated into palisade and spongy tissue, but when it is acicular the mesophyll is uniform throughout, consisting of parenchymatous cells with curiously infolded walls: the acicular leaves (Abietineæ) have a single central vascular strand enclosing two bundles which give off no branches; in the flattened leaves there may be several ribs which either do (*e.g.* Ginkgo) or do not (*e.g.* Dammara, Araucaria) branch in the lamina, and in all these cases the bundles end blindly; in Gnetum the leaf, and in Stangeria the leaf-pinna, has a midrib and pinnate venation; the multicostate leaf of Welwitschia has parallel venation. A remarkable feature in the structure of the leaf is the presence, in all the genera, of a tissue, termed *transfusion-tissue* (p. 169), which consists of parenchymatous cells, some of which contain no protoplasm and have pitted walls, being in fact tracheides, whilst others contain protoplasm and have unpitted walls: in the Abietineæ this tissue is a development of the pericycle of the vascular strand,

and is surrounded by a well-marked endodermis; in the other genera it appears to be specially differentiated mesophyll frequently (*e.g.* Cycas, Podocarpus, Cephalotaxus) consisting of cells elongated transversely to the long axis of the leaf: the use of the transfusion-tissue is to compensate for the absence of a much-branched vascular system in the leaf, the tracheidal cells serving to distribute water from the xylem of the bundles to the mesophyll, the other cells serving to convey organic substances formed in the mesophyll to the phloem of the bundles.

The *Root* grows in length by means of a growing-point differentiated into dermatogen, plerome and periblem, and root-cap as in Dicotyledons (see p. 154); there are commonly two xylem-bundles in the stele: the cambium-ring is formed in the usual way: the phellogen is derived from the pericycle; in many cases the cortical cells, other than those of the endodermis, show thickenings on their radial walls similar to those of the endodermis-cells; this is either confined to a single (penultimate) layer of the cortex (*e.g.* Cupressus, Thuja, Biota, Taxus, Cephalotaxus, Ginkgo), or it extends to several layers (*e.g.* Sequoia, Taxodium, Juniperus, Araucaria): the epiblema is generally devoid of root-hairs, but these are abundant in Taxus.

General histological peculiarities. In all the Coniferæ, except Taxus, *resin-ducts* (see p. 139) are present: they are always to be found in the leaves and in the cortex of the stem, sometimes also in the pith of the stem (Ginkgo), in the primary wood (Pinus, Larix), or in the primary bast (Araucaria); they are absent from the root in many genera (Cryptomeria, Taxodium, Podocarpus, Dacrydium, Tsuga, Cunninghamia, Ginkgo), and when present they never occur in the cortex, but are situated in the primary wood (Pinus, Larix), in the primary bast (Araucaria), or as a single canal in the centre of the conjunctive tissue (Cedrus, Abies, Pseudolarix): they are formed also in the secondary wood (Pinus, Picea, Larix) or in the secondary bast (Cupressus, Thuja, Araucaria) of both stem and root. Mucilage-ducts, resembling the resin-ducts of the Coniferæ, occur in the cortex of the stem in the Cycadaceæ.

The bast of the Gymnosperms resembles that of the Pteridophyta, and differs from that of the Angiosperms, in that it contains no companion-cells (see p. 137), the function of these cells being performed by certain cells belonging either to the medullary rays (Abietineæ, some Cupressineæ and Taxodineæ) or to the bast-parenchyma (Araucarineæ, Taxoideæ, some Cupressineæ and Taxodineæ, the Cycadaceæ and Gnetaceæ).

A remarkable feature in the histology of Welwitschia is the presence in the ground-tissue of large thick-walled fibrous cells, called *spicular cells*, in the walls of which crystals of calcium oxalate are deposited; the occurrence of these crystals in the cell-walls is common throughout the class (Fig. 65).

The General Morphology of the Reproductive Organs. The reproductive organs are microsporangia (pollen-sacs) and macrosporangia (ovules): the microsporangia are always borne on sporophylls, but the macrosporangia are sometimes borne directly on the axis (*e.g.* macrosporangia of Taxeæ and of the Gnetaceæ): they are developed on distinct shoots, and frequently on distinct plants (*e.g.* Cycadaceæ: some Coniferæ, such as most Araucarineæ and Taxeæ; Gnetaceæ generally).

Certain shoots are more or less clearly differentiated as *flowers*; the only exception being Cycas in which there is no proper macrosporangiate flower. The flower is always monosporangiate: its structure varies widely; it may consist merely of a terminal sporangium invested by a few small bracts (*e.g.* macrosporangiate flower of Taxeæ); of a terminal sporangium with a rudimentary perianth (macrosporangiate flower of Gnetacæ); of one or more sporophylls borne on a short axis and surrounded by a perianth (microsporangiate flower of Gnetaceæ); or of a larger or smaller number of sporophylls arranged on an elongated axis, the whole forming a cone.

In the Gnetaceæ the flowers are arranged in spicate inflorescences, and are situated in the axils of bracts which are more highly developed in this order than in any other Gymnosperms.

The *Sporophylls* are of two kinds, distinguished by the nature of the sporangia which they respectively bear, as microsporophylls and macrosporophylls. When the flower is a cone, the sporophylls have a general resemblance to scaly leaves: in other flowers (Taxeæ, Cycas, Gnetaceæ) they have various and specialised forms.

The *microsporophyll* (stamen) occurs in its simplest form in the Cycadaceæ, where it is a large stout scale bearing usually an indefinite number of microsporangia on its under surface. In some of the Coniferæ (*e.g.* Pinus), the microsporophyll essentially resembles that of the Cycadaceæ, though it is much smaller (in proportion with the smaller flowers) and bears only two microsporangia. In the other Coniferæ the microsporophylls, bearing 2–15 sporangia, show more or less distinct differentiation into a stalk bearing a terminal leafy expansion, until, in Taxus, a stage is reached where the microsporophyll consists of a stalk bearing a peltate lamina, on the under surface of which the sporangia are developed. In other words, the microsporophyll consists of a *filament* bearing a sorus of sporangia which constitutes an *anther* (see p. 432). In all cases the microsporangia are developed on the morphologically under (dorsal) surface of the sporophyll.

The gradual differentiation of the microsporophyll, which can be traced in the Coniferæ, leads on to the more complete differentiation and specialisation which obtains in the Gnetaceæ and in the Angiosperms. In Gnetum, however, there are no microsporophylls.

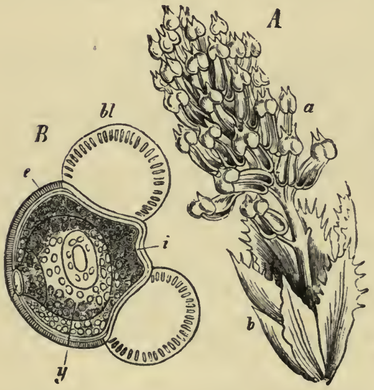

Fig. 296.—*A* Microsporophyllary (or staminal) flower of *Abies pectinata*; *b* scaly bracts; *a* microsporophyll with two microsporangia (pollen-sacs). *B* Microspore (pollen-grain) (highly mag.); *e* exine expanded into two hollow vesicles *bl*); *y* male prothallium. (After Sachs.)

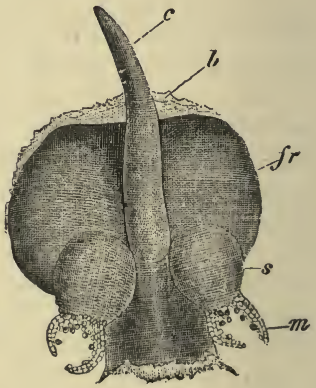

Fig. 297.—*Pinus sylvestris* (×7: after Strasburger). Macrosporophyll *b*, bearing on its upper surface the placental scale *fr*, which bears two ovules *s* at its base; *c* apophysial projection of the placental scale; *m* prolonged integument of the ovule within which pollen-grains have lodged.

The *macrosporophyll* (carpel) appears in a simple, yet typical, form in Cycas (see Fig. 303), the one Gymnosperm which has no distinct macrosporangiate flower. Here the carpels are essentially similar to the foliage-leaves, though they are smaller, of a yellow colour, and of a somewhat different form: they are, in fact, developed at the growing-point of the stem in the place of a whorl of foliage-leaves. The few sessile macrosporangia are borne laterally on the lower part of the sporophyll.

In the other Cycadaceæ, the macrosporophyll is a stout scaly leaf, thickened at its outer end, bearing usually two lateral ovules, one on each side.

In the Coniferæ, the simplest form of macrosporophyll is to be found in Dammara (Araucarineæ), for instance, where it is simply a scaly leaf bearing a single macrosporangium on its upper surface: in other forms the superior surface of the macrosporophyll is clearly marked out, by outgrowths of various kinds, into an apical and a basal half, the latter alone bearing the (1–7) macrosporangia (*e.g.* Taxodineæ, Cupressineæ): in the Abietineæ (Pinus, Larix, etc.) the sporangiferous structure of the preceding families is developed from the base of the carpel as a *placental scale*, which is much larger than the carpel itself, and bears the two macrosporangia on its upper surface. In most Podocarpeæ, the macrosporophyll is likewise differentiated into an apical and a basal half, the latter being much thickened, but here it is the apical portion which bears the single macrosporangium. In the Taxeæ the macrosporophylls are rudimentary (*e.g.* Phyllocladus, Cephalotaxus) or absent (*e.g.* Torreya, Taxus); even when present they do not bear the macrosporangia.

In the Gnetaceæ there are no macrosporophylls.

The *microsporangia* (pollen-sacs) are borne, in nearly all cases, on the lower (dorsal) surface of a sporophyll; they may be numerous (about 1,000) as in some Cycadaceæ; or few (2–15) in the Coniferæ and Gnetaceæ: scattered (some Cycads), or more commonly grouped into one or more sori, with more or less well-developed placental tissue; either imbedded in the tissue of the sporophyll (*e.g.* Abietineæ), or freely suspended (*e.g.* Araucaria, Ginkgo): in the Cupressineæ, the sporangia, when young, are covered by an outgrowth of the under surface of the sporophyll which is comparable to the indusium of Ferns. In Gnetum, as there is no microsporophyll, the two microsporangia are borne on the apex of the floral axis.

The structure of the microsporangium is simple: it is unilocular; it contains, at an early stage, a mass of spore-mother-cells derived from the archesporium, surrounded by a layer of tapetal cells also derived from the archesporium, and by a wall consisting of one, two, or more, layers of cells: each spore-mother-cell gives rise to four microspores, which are usually tetrahedral, but bilateral in the Cycads. The dehiscence is generally longitudinal.

The *microspores* (pollen-grains) present no special features beyond the fact that in some genera of Coniferæ (*e.g.* most Abietineæ and Podocarpeæ) the exine is dilated into two hollow expansions which lighten the pollen-grains and facilitate their dispersal by the wind.

The *macrosporangia* (ovules) are borne either terminally on a floral axis (*e.g.* Taxeæ, Gnetaceæ), or on the upper surface of a macrosporophyll; on the floral axis they are borne singly, on the sporophylls their number varies (1–7): they are orthotropous and sessile, the micropyle being directed either towards the axis of the cone (in Abietineæ, Podocarpeæ), or away from it (Cupressineæ): they have a single integument, though in some genera (most Taxoideæ) an arillus is eventually developed. The macrosporangia are indehiscent.

The archesporium consists of one or more hypodermal cells of the micropylar end of the nucellus: from the archesporium the sporogenous cells are developed, as also tapetal cells. By the formation of several layers of tapetal cells, and also by the repeated periclinal division of the micropylar epidermis, the sporogenous cells come to be deeply placed in the nucellus, being surmounted by a considerable mass of nucellar tissue which, in the Cycadaceæ, is hollowed out at the apex to form the *pollen-chamber*. There may be a considerable mass of sporogenous cells (Cycadaceæ, etc., see p. 438), a condition which recalls that in the higher Pteridophyta, or there may be a single sporogenous cell (Abietineæ). The sporogenous cell, or one of the sporogenous cells, grows rapidly, causing the absorption of the adjacent cells, and is the mother-cell of the macrospore: in some cases, where there are many sporogenous cells, several of them may begin to grow in this way, but as a rule, one gains the upper hand so that eventually only one mother-cell is present.

The *macrospore* (embryo-sac) is developed singly in the macrosporangium, by the growth and maturation of the mother-cell which does not undergo division into four as in the Pteridophyta. In the Cycadaceæ the wall of the macrospore, like that of spores generally, is differentiated into two layers, the outer of which is cuticularised.

Pollination. The microspores are conveyed by the wind from the microsporangiate to the macrosporangiate flowers, the Gymnosperms being anemophilous, and they come into direct relation with the micropyle. In the case of cone-flowers, the scales separate at the time of pollination, to permit of the pollen-grains being blown in between them. The micropyle of the ovule secretes a mucilaginous liquid which catches one or more of the pollen-grains: by the gradual evaporation of this liquid, the pollen-grain is drawn down the micropyle and is lodged on the apex of the nucellus, where it germinates.

Embryogeny of the Sporophyte. The Gymnosperms are all meroblastic and have a suspensor, with the single exception, in both respects, of Ginkgo: they are frequently polyembryonic (most Cupressineæ, Abietineæ, and Gnetaceæ).

The most peculiar type of development is that which is characteristic of the Cycadaceæ, of Ginkgo among Coniferæ, and of Ephedra among Gnetaceæ. In these plants the germination of the oospore begins with repeated nuclear division followed by free cell-formation which leads, in the Cycadaceæ, to the production either of a layer of cells round the wall of the archegonium (Cycas), or of a mass of cells occupying its lower end (Ceratozamia), a considerable cavity being left vacant in both cases: in Ephedra, several (2–8) loose spherical cells are formed in a similar manner, in the oospore, each with its own proper wall: and in Ginkgo, it becomes completely filled with a mass of cells forming a compact tissue. In the Cycadaceæ, the embryonic cells at the lower end of the oospore grow out into the endosperm, forming a suspensor at the free end of which the body of the embryo is developed. In Ephedra, each of the cells elongates into a suspensor which grows out into the endosperm and produces an embryo. In Ginkgo, the mass of cells constitutes the embryo itself; there is no suspensor, but the embryo, in the course of its growth, breaks out of the archegonium into the endosperm. In the Coniferæ (except Ginkgo) the type of development is essentially the same throughout, though with slight variations. In the Abietineæ the nucleus of the oospore descends towards the lower end of the cell, and divides into two, and each of these again into two; cell-formation takes place, walls being formed in two planes at right angles to each other, so that the lower end of the oospore is occupied by a group of four cells lying in one plane; these cells then divide by transverse walls, so that three tiers of four cells each are formed; of these, each cell of the middle tier grows out into a long unicellular suspensor; those of the upper tier simply maintain the connexion of the suspensors with the rest of the oospore; those of the lowest tier, whilst also contributing to the suspensors, each give rise to an embryo from the cells

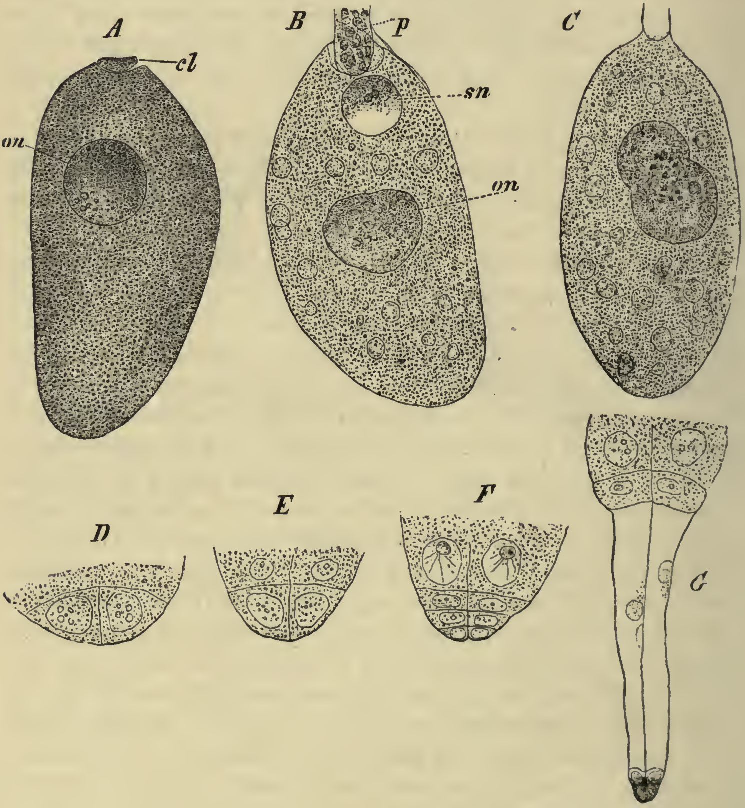

FIG. 298.—Fertilisation, and early stages in the embryogeny, of *Picea excelsa* (× 90; after Strasburger). *A* Oosphere, with nucleus *on*, and canal-cell *cl*. *B* Fertilisation in progress: *p* pollen-tube; *sn* nucleus (male pronucleus) of the male cell now in the oosphere; *on* female pronucleus. *C* Fusion of male and female pronuclei. *D* Commencing cell-formation at the chalazal end of the oospore; *E* a further stage: *F* three tiers of four cells each have been formed: *G* the cells of the middle tier have elongated into suspensors, bearing the single embryo at their lower end.

at the base of which one or more *embryonal tubes* are developed which grow backward along the suspensor. *Picea excelsa* departs from this type in that the suspensors remain coherent, bearing at

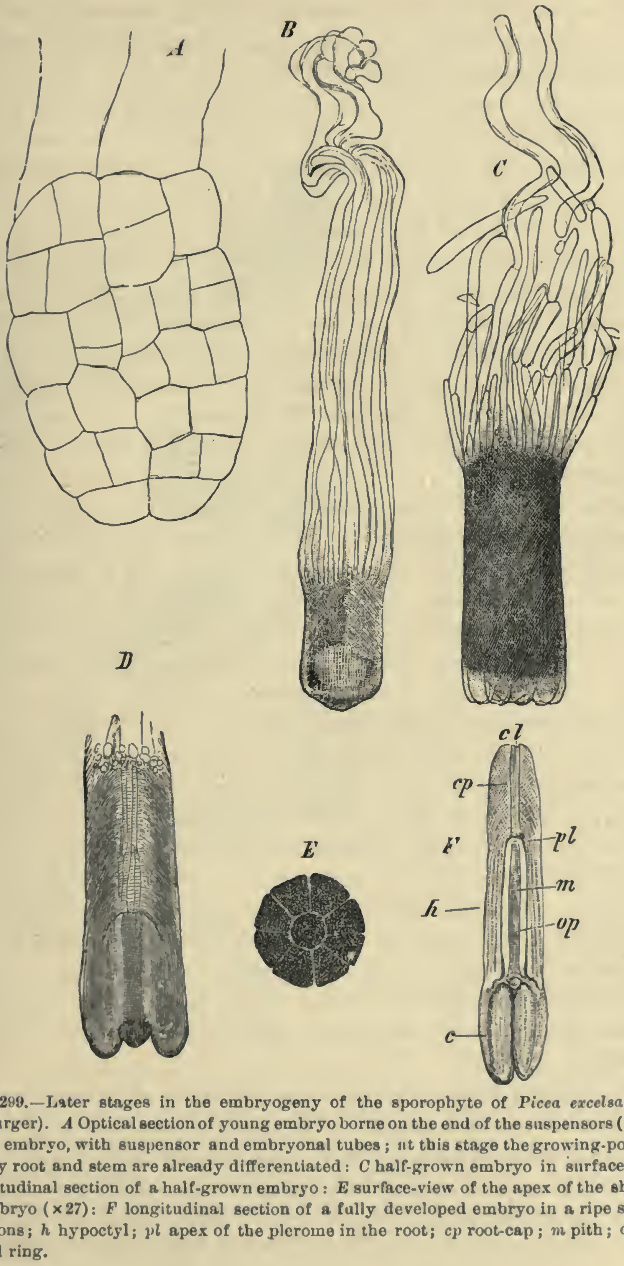

FIG. 299.—Later stages in the embryogeny of the sporophyte of *Picea excelsa* (after Strasburger). *A* Optical section of young embryo borne on the end of the suspensors (×240): *B* older embryo, with suspensor and embryonal tubes; at this stage the growing-points of primary root and stem are already differentiated: *C* half-grown embryo in surface-view: *D* longitudinal section of a half-grown embryo: *E* surface-view of the apex of the shoot of this embryo (×27): *F* longitudinal section of a fully developed embryo in a ripe seed; *c* cotyledons; *h* hypoctyl; *pl* apex of the plerome in the root; *cp* root-cap; *m* pith; *op* procambial ring.

their end the cells of the lowest tier which develope into but a single embryo, whereas in the typical Abietineæ four embryos originate from each oospore.

Among the Cupressineæ, the first step is the formation of three cells one above the other at the lower end of the oospore: in *Thuja occidentalis* only the two upper cells undergo longitudinal division, and, consequently (as in *Picea excelsa*) only a single embryo is developed from each oospore: in Juniperus, all three cells undergo longitudinal division, so that four embryos are here developed from each oospore. In this group the cells of the uppermost tier elongate to form the suspensors: those of the middle tier contribute to the length of the suspensors, and also give rise to short embryonal tubes which invest the suspensor for some distance, as also the base of the embryo: the cell or cells of the lowest tier give rise to the embryo (Thuja) or embryos (Juniperus).

In the Taxeæ, as represented by Taxus and Cephalotaxus, the embryogeny closely resembles that of Thuja, though there is not the same degree of constancy; two or three tiers of cells, varying in number, are formed at the lower end of the oospore; of these, the uppermost tier (Taxus) or second tier (Cephalotaxus) grow out into the (usually six) suspensors; those of the lower or lowest tier form the single embryo and the embryonal tubes.

The embryogeny of the Gnetaceous genera Gnetum and Welwitschia is peculiar: in Welwitschia the oospore, whilst still enclosed in the wall of the archegonium, undergoes a transverse division at its base, which cuts off a small flat cell as the embryo-cell; the wall of the archegonium continues to grow, and forms the suspensor; the embryo-cell gives rise to the single embryo and to a number of embryonal tubes which invest the lower portion of the suspensor: in Gnetum, so far as the embryogeny is known, it appears that an embryo-cell is formed at the end of the suspensor, as in Welwitschia, from which the embryo and the embryonal tubes are also developed; the suspensor appears to branch, each branch bearing an embryo.

The growing-point of the stem is developed at the anterior end of the embryo: two species of Coniferæ (*Cephalotaxus Fortunei*, *Araucaria brasiliana*) present the peculiarity that the growing-point is not quite terminal, but is covered by a small group of cells which are subsequently thrown off: in some cases (Cupressineæ, *Pinus Strobus*, apparently Taxus and Gnetum, and occasionally

Ephedra), there is a two-sided apical cell in the growing-point at its first development.

The cotyledons vary in number: one, in Ceratozamia, and sometimes in other Cycadaceæ; two, in the Cycadaceæ generally, in the Cupressineæ generally, in some Araucarias, in the Taxoideæ, and in the Gnetaceæ; in the Cupressineæ sometimes 3–5; in the Taxodineæ 4–9; in the Abietineæ 5–15. The cotyledons are generally epigean: they are hypogean in the Cycadaceæ, as also in Araucaria (sect. Colymbea) and in Ginkgo among the Coniferæ: in the Cycadaceæ, and in Ginkgo, the two hypogean cotyledons are closely coherent at the apex, whereas in these Araucarias the cotyledons are free.

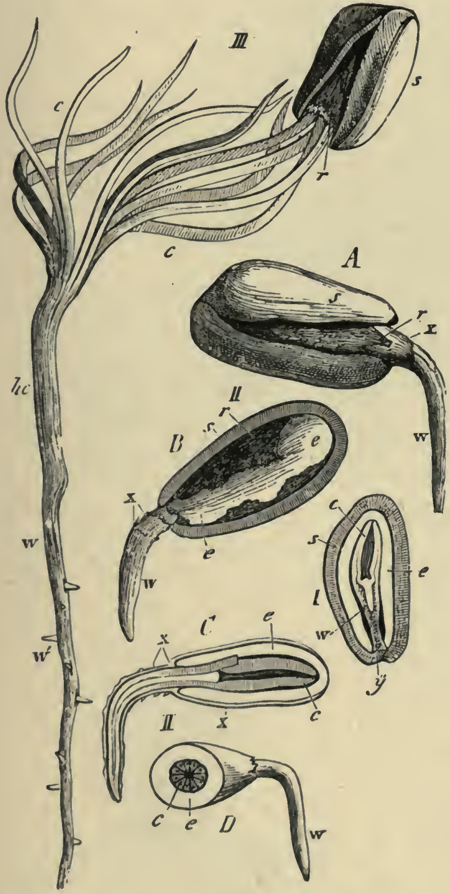

Fig. 300.—Germinating seeds of *Pinus Pinea*: *I* first stage, in longitudinal section: *II* second stage, with protruding radicle; *A* external view; *B* view after removal of half the seed-coat; *C* longitudinal section, without seed-coat; *D* transverse section, without seed-coat; *III* germination is here completed, the cotyledons having expanded, and the hypocotyl elongated: *s* seed-coat; *e* endosperm; *w* radicle; *c* cotyledons; *y* micropyle; *r* red membrane (remains of nucellus); *x* the embryo-sac.

The growing-point of the root is in all cases differentiated endogenously, at some distance from the posterior end of the embryo.

THE GAMETOPHYTE.—As the Gymnosperms are heterosporous, the sexual generation is represented by two individuals, a male and a female.

The *Male Individual* is a prothallium developed from the microspore as described on p. 448. It consists of two or more cells, one of which grows out into a pollen-tube (see Fig. 290).

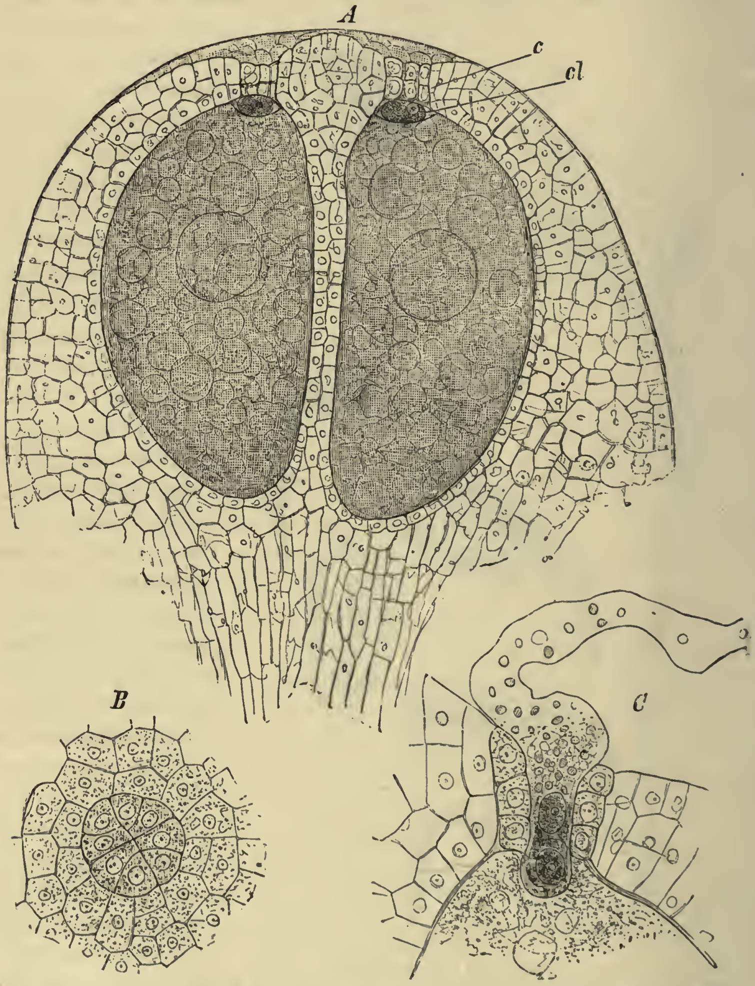

Fig. 301.—*A* Longitudinal section of the micropylar portion of the female prothallium of *Picea excelsa* showing two archegonia (×100): *c* neck of archegonium; *cl* canal-cell. *B* Surface-view of unopened neck of an archegonium (×250). *C* Pollen-tube penetrating to the oosphere through the neck of the archegonium (×250). (After Strasburger.)

The *male organ* is a rudimentary antheridium consisting of two cells, the *stalk-cell* and the *generative cell.*

The *male cell* is derived from the generative cell of the antheridium which travels into the pollen-tube (see Fig. 289); this cell undergoes division into two similar cells, near the apex of the pollen-tube, both of which are, as a rule, functional male cells equivalent to spermatozoids; in Taxus, however, the two cells differ in size, and it is only the larger one that is a functional male cell. The male cell is of somewhat spherical or oval form. When, as in Juniperus, and other Cupressineæ, several archegonia are fertilised by means of a single pollen-tube, repeated cell-division takes place in the pollen-tube.

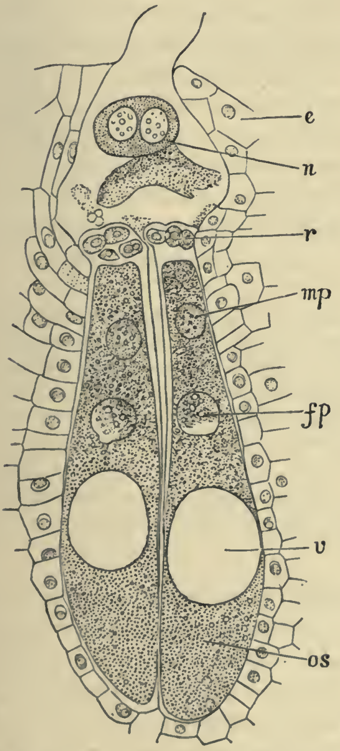

Fig. 302.—Fertilisation of two archegonia by means of a single pollen-tube in *Juniperus virginiana* (×230: after Strasburger): *e* prothallial tissue; *r* neck of archegonium; *n* nucleus in the pollen-tube; *mp* male pronucleus, *fp* female pronucleus, in the oosphere; *v* vacuole in the oosphere; *os* lower part of oosphere.

The *Female Individual* is a prothallium (sometimes called endosperm) developed within the macrospore. The germination of the macrospore begins with the division of its nucleus; nuclear division is repeated until a large number of nuclei are formed, lying in the parietal protoplasm of the spore; free cell-formation then takes place, walls being formed between the cells so that the interior of the macrospore is lined by a layer of cells which grow and divide until the cavity of the macrospore is entirely filled. It is characteristic of Gymnosperms that the development of the prothallium is uninterrupted, and that it is completed, except in Gnetum, before the female organs are developed and, consequently, before fertilisation can have taken place.

The female prothallium is a mass of parenchymatous tissue, which does not, as a rule, escape to any extent from the spore, and which, in consequence of the exclusion of light, is destitute of chlorophyll; the only exception to this rule is offered by the Cycadaceæ where, if the female organ is not fertilised, the prothallium, resuming its growth, protrudes through the micropyle and turns green in the light.

The *female organ* is an archegonium, and is developed from a single superficial cell of the female prothallium at its micropylar end. The mother-cell generally divides transversely into two; an upper, the *neck-cell*; a lower, the *central cell*: the neck-cell usually divides, by two vertical walls, into four cells, which form the neck; the central cell grows, and divides transversely at its upper end so as to cut off a small cell, the *canal-cell*, which lies in the canal formed by the separation of the neck-cells, and a large cell which is the *female cell or oosphere* (Figs. 301, 302).

The most striking deviations from the development of the archegonium, as described above, are the following: the mother-cell does not divide but becomes the central cell of a neckless archegonium, either with a cell-wall (Welwitschia) or without a cell-wall (Gnetum); the neck-cell remains undivided (*Tsuga canadensis*); the neck-cell divides only once, longitudinally, so that the neck consists of two cells (*e.g.* Cycadaceæ, Ginkgo); by a third vertical division of the neck-cell, the neck comes to consist of eight cells, all in one plane (some Cupressineæ); by one or more transverse divisions, the neck consists of two or more tiers of cells (*e.g. Pinus Pinaster* with four cells in each tier; *Picea excelsa* with eigth cells in each tier).

The number of archegonia developed on the female prothallium varies from a small number (3–5) in the Abietineæ, to a large number (20–60) in Welwitschia and Gnetum. The archegonia are either scattered (Abietineæ), or in a group (Cupressineæ): when scattered, the central cells are surrounded by a layer of small cells belonging to the prothallium; when in a group, the central cells are in actual contact and have a common investment of small cells.

In Welwitschia, the unicellular archegonia grow out into filaments, at the upper end, which make their way through the tissue of the nucellus toward the micropyle.

The *female cell* or *oosphere* is a relatively large nucleated cell, the protoplasm of which is so highly vacuolated that it presents a frothy appearance.

Fertilisation. When the microspore has reached the apex of the nucellus, it developes a pollen-tube which penetrates the tissue of the nucellus, making its way to the archegonia which have been, or are being, developed on the prothallium inside the macrospore; the pollen-tube at length reaches the macrospore, pierces its wall, and enters the neck of an archegonium (when scattered), or spreads out over the necks of a group of archegonia; a male cell is forced out through the tip of the pollen-tube into the oosphere, or into each of the oospheres of a group of archegonia so that one male organ fertilises several archegonia (Fig. 302); the act of fertilisation is completed by the fusion of the male pronucleus with the female pronucleus, to constitute the nucleus of the oospore.

In Welwitschia the process is somewhat different; here fertilisation takes place in the tissue of the nucellus, where the pollen-tubes meet and fuse with the filamentous outgrowths of the archegonia.

The Results of Fertilisation.

1. *The fruit.* In all the Gymnosperms which have a cone-like macrosporangiate flower (Cycadaceæ, except Cycas; Coniferæ, except Taxeæ), one effect of fertilisation is to cause more or less considerable growth in the macrosporophylls, or in the placental scales, as also tissue-change resulting in their becoming woody (*e.g.* Pinus, Abies, etc.) or fleshy (*e.g.* Juniperus), the product being the fruit.

The fruit-cone, in most cases, sets free the seed by the separation of the macrosporophylls, or of the placental scales, which fall off from the axis of the cone, leaving it bare (most Cycadaceæ, Araucaria, Abies, Agathis, Cedrus); or they merely separate enough to let the seeds fall out, and then the cones either remain on the tree (*e.g.* Larix), or, as is more commonly the case, drop off entire. However, where the fruit is a berry-like cone (*e.g.* Juniperus), the macrosporophylls do not separate, and the dispersion of the seed depends on the fruit being eaten by animals.

In other cases the effects of fertilisation extend to the bracts (Ephedra) or to the perianth (Gnetum), causing them to grow and become succulent.

2. *The seed* is albuminous in all Gymnosperms, the single straight embryo being imbedded in the endosperm (see Fig. 300 *I*) in all cases, also, some portion of the nucellar tissue persists as perisperm, amounting, in the Cycadaceæ and Coniferæ, to little more than a membranous layer, but in the Gnetaceæ (at least in Ephedra and Welwitschia) it is more considerable.

The development of the seed-coats varies widely. In the Cycadaceæ the testa consists of two layers, an outer fleshy and succulent, and an inner hard and woody, so that the seed bears a superficial resemblance to a fruit such as a plum: in those Coniferæ in which the seeds are produced in a cone-fruit, the testa is hard and tough; but in those in which the seed is exposed from the first, the testa is either fleshy (*e.g.* Ginkgo, Cephalotaxus), being developed after the manner of that in the Cycadaceæ, or it is hard, and is invested by a succulent aril (*e.g.* Taxus, Podocarpus). In those Coniferæ with woody cones (*e.g.* Abietineæ, Araucarineæ, most Cupressineæ) the seed is usually winged, either by means of a membranous outgrowth of the testa, or (Abietineæ) by the adhesion to the seed of a thin strip of tissue, split off from the surface of the placental scale. Among the Gnetaceæ, the testa is hard and woody in Ephedra and Gnetum; in Welwitschia the seed is enclosed by the expanded perianth, which acts as a wing.

Classification of the Gymnospermæ.

The class contains the following three orders:—

1. CYCADACEÆ: the trunk is generally unbranched: the leaves are large and branched: no vessels in the secondary wood.

2. CONIFERÆ: trunk much branched: leaves many, small, and unbranched: no vessels in the secondary wood.

3. GNETACEÆ: habit various: flowers have a rudimentary perianth: there are vessels in the secondary wood.

Order 1. **Cycadaceæ.** The Cycadaceæ are plants which, in many respects, show affinity with the Ferns, while, on the other hand, they resemble the Palms in external appearance. The stem is tubercular or cylindrical. The vegetative leaves are of two kinds; scaly leaves, brown and dry, closely covering the surface of the stem; foliage-leaves, pinnate, of a leathery consistency, produced annually or at a longer interval, forming a crown at the top of the stem; the foliage-leaves are generally developed expanded, but in Cycas the pinnæ are circinate in vernation, as is also the phyllopodium in Stangeria and Zamia.

The diœcious flowers are produced, either singly or several together, at the apex of the stem; they are cones (except Cycas). The development of the cones does not arrest the growth in length of the stem: hence the stem may be regarded as a sympodium, its growing-point being maintained by either dichotomous or lateral branching (pp. 33, 35). The macrosporophylls of Cycas do not constitute a true flower, since they are not borne, as in the other genera, on a special axis, but simply take the place of a whorl of foliage-leaves. The cones consist of an elongated axis, bearing numerous spirally-arranged scaly sporophylls, which vary in number from 30 to 600. The microsporophylls bear, on the under surface, usually numerous (2 to 1000) microsporangia, either scattered or in sori (Cycas, Stangeria, Zamia). The macrosporophylls bear two orthotropous macrosporangia, one on each flank, developed upon the peltate terminal lamina; but the exceptional macrosporophylls of Cycas (see Fig. 303) may bear as many as five macrosporangia.

The macrosporangia are all sessile, and have a single integument, and are of considerable size; those of Cycas are as large as a plum before fertilisation.

In the coniferous genera, the macrosporangiate flower becomes the fruit; that is, a dry cone, the sporophylls of which fall away, and so set free the seeds. In Cycas, the sporophylls bend outwards and drop off, bearing the seeds. The seed is covered by a testa, developed from the integument of the ovule, which is succulent externally and stony internally. It contains a single straight embryo, on a coiled suspensor, lying in the endosperm. The embryo, has generally two cotyledons (one in Ceratozamia, and occasionally in other genera also), which are hypogean, remaining in the seed.

The Cycadaceæ, of which there are nine genera, and about seventy-five species, are all tropical or sub-tropical. Cycas is a native of the East Indies and Australia; Macrozamia and Bowenia, of Australia; Encephalartos and Stangeria, of Africa; Zamia, Ceratozamia, Dioon, and Microcycas, of tropical America.

Cycas is clearly distinguished from the other genera by its peculiar macrosporophylls, involving the absence of a macrosporangiate flower; Bowenia is characterised by its bi-pinnate leaves; Stangeria by the pinnate venation of its leaves; the other genera, by the form of their sporophylls.

Order 2. **Coniferæ.** This order includes the Pines, Firs, Cypresses, Yews, etc., which, for the most part, are extra-tropical, inhabiting more especially the northern hemisphere.

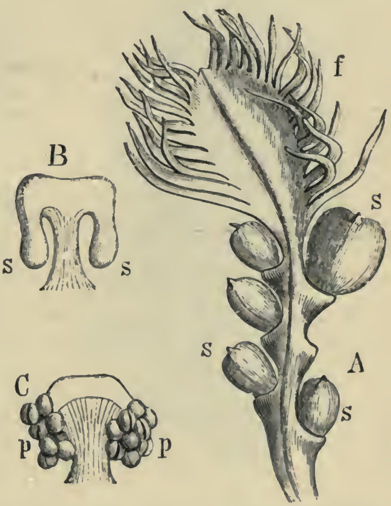

Fig. 303.—Sporophylls of Cycads. *A* macrosporophyll of *Cycas revoluta* (¼ nat. size): *f* pinnæ; *s* ovules. *B* Macrosporophyll of *Zamia muricata*, with two ovules (*s*); *C* microsporophyll of this species with numerous microsporangia (*p*).

The conspicuous features of their morphology are the regular monopodial branching of the stem, the small (often acicular) simple leaves, and the taproot. In their histology, these plants resemble the Dicotyledons in that the stem grows in thickness by a normal cambium-ring; but the vascular tissue of the wood consists entirely of tracheides with bordered pits. The presence of resin-ducts is another characteristic feature.

The flowers are always monosporangiate; some genera are diœcious. The microsporangiate flower is a cone, consisting of an elongated axis bearing microsporophylls (Fig. 304), which are generally somewhat peltate in form. Each microsporophyll bears two or more microsporangia on its under (dorsal) surface. The macrosporangiate flower is also a cone in certain cases (Pinoideæ, Fig. 305), in which case the macrosporophylls bear the macrosporangia; in other cases there is a less perfect cone, or none at all (Taxoideæ, see Fig. 308), the macrosporophylls are either rudimentary or absent, and the macrosporangia are generally borne on the axis.

In some genera (*e.g.* Pinus, Juniperus) the seed takes two years to ripen; in the first year, pollination takes place, and the pollen-tube begins to grow through the tissue of the nucellus; in the second year, after a period of rest, the pollen-tube completes its growth, reaches the archegonium, and fertilises the oosphere; as a consequence, the embryo is developed, and the ovule is changed into a seed.

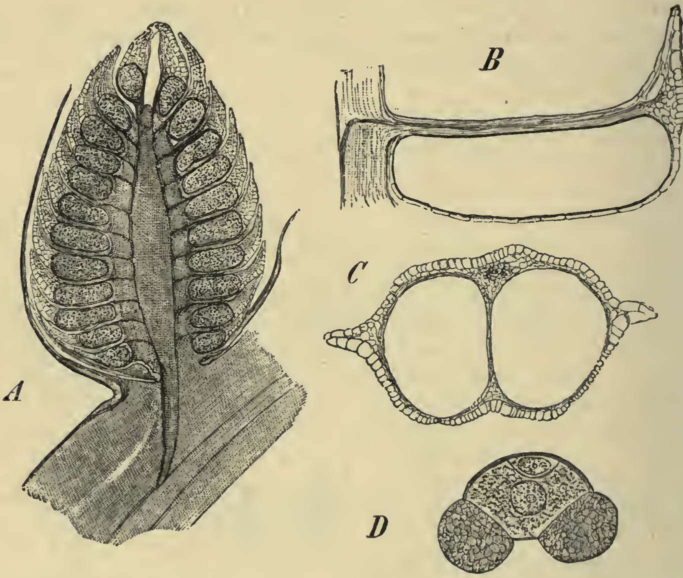

FIG. 304.—*Pinus montana* (*Pumilio*). *A* Longitudinal section of a microsporangiate flower (× 10). *B* Longitudinal section of a microsporophyll, showing the cavity of one pollen-sac (× 20). *C* Transverse section of a microsporophyll, showing the cavities of both pollen-sacs. *D* Germinating two-celled microspore of *Pinus sylvestris*, showing the expansions of the exine (× 400). (After Strasburger.)

In spite of the fact that so many of the Coniferæ are polyembryonic (see p. 471), and that each ovule contains several archegonia, the ripe seed contains only a single embryo, though occasionally two are found (*e.g.* Ginkgo). The embryo has two, or more, cotyledons, which are epigean, except in Araucaria, sect. Colymbea, and in Ginkgo, where they are hypogean.

The order, which includes 34 genera and about 350 species, may be naturally divided into the two sub-orders, Pinoideæ and Taxoideæ, based upon the structure of the macrosporangiate flower; each of these sub-orders includes several families.

Sub-order I. Pinoideæ. The macrosporangiate flowers are cones; the seed has a woody or leathery testa, is enclosed between the macrosporophylls or the placental scales, and has no aril.

Fam. 1. *Araucarineæ:* usually diœcious; macrosporophyll simple, bearing a single macrosporangium. The microsporophyll bears 5 to 15 free microsporangia; microspores without expansions of the exine; all leaves arranged spirally; cotyledons 2–4.

This family includes the two genera, Agathis (Dammara) and Araucaria. Agathis inhabits the Malayan islands, parts of Australia, New Zealand, Fiji Islands; *A. australis* is the Kauri Gum-tree: Araucaria inhabits South America (*A. brasiliana*, Brazil; *A. imbricata*, Chili), and Australasia (*A. excelsa*, Norfolk Island).

Fam. 2. *Abietineæ:* monœcious; on its upper surface at the base, the macrosporophyll bears a large placental scale on the upper surface of which two inverted macrosporangia are borne. The ripe seed has two wings derived from tissue of the placental scale; the microsporophyll bears two microsporangia; microspores usually have expansions of the exine; all leaves arranged spirally; cotyledons, more than 2, commonly 5, sometimes as many as 15.

The most important genera may be distinguished as follows:—

A. No dwarf-shoots; placental scales flat; seed ripens in one year; stem bears whorled branches.

1. Fruit-cones erect, falling to pieces when ripe; foliage-leaves flat, cylindrical at the base, and not decurrent; placental scales about the same length as the macrosporophylls . . . . . *Abies.*

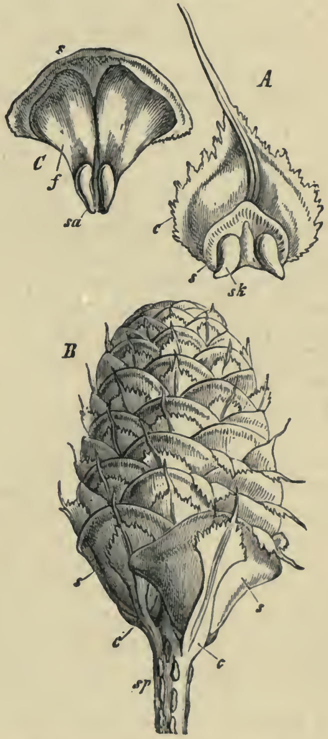

Fig. 305.—*Abies pectinata.* *A* Carpel *c*, seen from above (ventral surface), showing *s* the placental scale, and *sk* the two ovules (mag.). *B* Mature cone (nat. size); *sp* axis; *c* carpel; *s* enlarged placental scale. *C* Ripe placental scale (*s*) isolated, seen from above; *sa* the two seeds, each with a wing (*f*). (After Sachs.)

2. Fruit-cones pendent, falling off entire; foliage-leaves with decurrent projecting base.

(*a*) Leaves 4-angular; placental scales much longer than the macrosporophylls . . . . *Picea.*

(*b*) Leaves flat; placental scales longer or shorter than the macrosporophylls . . . . *Tsuga*

B. Long and dwarf-shoots.

1. Placental scales flat; foliage-leaves borne on both long and dwarf-shoots; branching of the stem irregular.

(*a*) Leaves annually deciduous; seed ripens in one year . *Larix.*

(*b*) Leaves persistent; seed ripens in two years . . . *Cedrus.*

2. Placental scales thickened externally into an apophysis: foliage-leaves confined to the dwarf-shoots: branches whorled . *Pinus.*

1. *Abies*, the Silver Firs. The foliage-leaves are flat, marked on the under surface with two longitudinal white streaks, and show in section two lateral resin-ducts: the macrosporangiate cone is developed in the axil of a leaf borne on a shoot of the previous year, at some distance from its apex, and when ripe falls to pieces so that the naked axis remains. To this genus belong *A. pectinata* (*A. alba*), the Silver Fir, the emarginate leaves of which stand out in a comb-like manner from the branches; *A. Nordmanniana*, from the Caucasus; *A. balsamea*, which produces Canada-balsam; *A. cephalonica*, which grows in Greece, and *A. Pinsapo*, which grows in Spain, both having pointed leaves which, in the latter species, are borne on all sides of the branches.

2. *Picea*, the Spruce Firs. The foliage-leaves are quadrangular, and have two lateral resin-ducts: the macrosporangiate cone is borne terminally on a shoot of the previous year, becomes pendent after fertilisation, thus enabling the seeds to drop out, and then falls off entire. To this genus belong *P. excelsa*, the Norway Spruce, the leaves of which are compressed laterally; in some species, however, the leaves are compressed vertically (*e.g. P. omorica*, in Servia, and *P. ajanensis*, in Eastern Asia), and are streaked with white on the upper surface. *P. alba* and *nigra* are the White and Black Spruces of North America.

3. *Tsuga*, the Hemlock Firs. The flat foliage-leaves are somewhat channelled above, with a midrib projecting on the under surface. In other respects this genus, more especially the Section Eutsuga, generally resembles Picea. In the Section Eutsuga (*e.g. Ts. canadensis*) the placental scales are much longer than the macrosporophylls; whereas in the section Pseudotsuga (*e.g. Ts. Douglasii*) the macrosporophylls are as long as, or longer than, the placental scales: in Eutsuga there is a single median resin-duct in the projecting midrib of the leaf.

4. *Larix*, the Larches. The deciduous leaves are arranged spirally on long shoots, and also in clusters on dwarf-shoots developed in the axils of the leaves of the long shoots of the previous year: the microsporangiate cones are borne terminally on leafless dwarf-shoots, the macrosporangiate cones terminally on leafy dwarf-shoots. *L. europæa* is the common Larch, a native of the Alps and Carpathians. The sub-genus Pseudolarix, including the single species *Ps. Kaempferi* (otherwise *Larix Kaempferi*), the Golden Larch, differs from the true Larches mainly in that its macrosporangiate cones fall to pieces when ripe: it is a native of China.

5. *Cedrus*, the Cedars. This genus differs from Larix in that the leaves, which are arranged in the same way, persist for more than one year, and in that the seed takes two years to ripen. The genus includes three species:

C. Libani, in Asia Minor; *C. atlantica*, in the Atlas mountains of North Africa: *C. Deodara*, in the Himalayas.

7. *Pinus*, the Pines. The thick placental scales are expanded at their free end into a flattened rhombic surface, the *apophysis*: the seed takes two years to ripen: the foliage-leaves persist for several years and are confined to dwarf-shoots which bear cataphyllary leaves at their bases, and are borne in the axils of the cataphyllary leaves of the long shoots of the same year: the primary branches are arranged in false whorls near the apex of the shoot of any one year, and the branches of a higher order are developed in the same manner: the microsporangiate cones take the place of dwarf-shoots at the base of a long shoot of the same year, and are closely packed: the macrosporangiate cones also occupy the place of dwarf-shoots near the apex of long shoots of the same year.

In the section Pinaster, the apophysis has a rhombic free surface with a central projection (umbo): it includes three sub-genera:—Pinea, characterised by the fact that each dwarf-shoot bears two leaves, with about twenty species, including *Pinus sylvestris*, the Scots Pine; *P. Laricio*, the Black Pines; *P. Pinaster*, the Cluster Pine of South Europe; *P. montana*, the Mountain Pines of Europe; *P. Pinea*, the Stone Pine of the South of Europe, the seeds of which are large and edible:—Tæda, where each dwarf-shoot bears three leaves, with about sixteen species, including *Pinus Tæda*, the Frankincense tree of North America:—Pseudostrobus, where each dwarf-shoot usually bears five leaves, with about ten North American species.

In the section Strobus, the dwarf-shoots usually bear five leaves, and the apophysis runs out into a projection (umbo) at its upper edge: it includes two sub-genera:—Eustrobus, with pendulous fruit-cones and winged seeds, including *Pinus Strobus*, the Weymouth Pine; *P. excelsa*, the Himalayan Pine; *P. Lambertiana*, the Sugar Pine, and *P. monticola*, both of California and Oregon:—Cembra, with erect or divergent cones and seeds without wings, including *Pinus Cembra*, the Stone Pine of Switzerland and Siberia; *P. flexilis*, of North America; and *P. parviflora*, of Japan.

Fam. 3. *Taxodineæ*: monœcious: the macrosporophyll is clearly differentiated into an outer and an inner (placental) half; the latter forms an outgrowth across the upper surface of the macrosporophyll, which may even reach the surface of the cone: seeds 2–9, either axillary and erect, or borne on the surface of the macrosporophyll and inverted, generally without a wing: microsporophylls bear 2–8 microsporangia: microspores with expansions of the exine: leaves arranged spirally.

Sciadopitys (*S. verticillata*), the Umbrella Pine of Japan, is the only member of the family which has long and dwarf-shoots, the latter being a single pair of confluent linear leaves; the placental outgrowth projects beyond the apex of the macrosporophyll, and bears a transverse row of about seven seeds at its base.—In Cunninghamia, the placental outgrowth is narrow and membranous.—In Athrotaxis, the Tasmanian Cypress, the placental outgrowth is a thick ridge.—Sequoia includes the two species of large Californian trees, *S. sempervirens*, the Californian Red-wood, and *S.* (*Wellingtonia*) *gigantea*, celebrated for the great height to which they grow (over 300 feet), with a circumference of 50–60 feet at the base; the placental outgrowth is a slight transverse ridge. In the preceding genera, the seeds are all borne on the placental region of the macrosporophyll and are inverted; in the following genera the seeds are axillary and erect. Cryptomeria has an erect fringed placental outgrowth.—Taxodium, is the deciduous Cypress of North America; its leaf-bearing twigs are thrown off each year (*T. distichum*), or persist for two years (*T. mexicanum*) : the placental outgrowth overgrows the macrosporophyll as the cone ripens.—Glyptostrobus is the Chinese Water Pine; it differs from Taxodium only in that the seed has a wing.

Fam. 4. *Cupressineæ*: monœcious, sometimes diœcious: macrosporophylls with a projecting placental outgrowth: seeds axillary, erect, often winged: microspores without expansions of the exine: leaves always arranged in whorls.

In the sub-family *Actinostrobinæ*, including the genera Actinostrobus, Callitris, and Fitzroya, the ripe cone is woody and the constituent macrosporophylls are arranged in a valvate manner.

In the sub-family *Thujopsidinæ*, including the genera Thujopsis and Thuja (incl. Libocedrus and Biota) the ripe cone is woody and the constituent macrosporophylls are arranged in an imbricate manner. The most familiar species are *Thuja occidentalis*, the American Arbor Vitæ, and *Thuja* (*Biota*) *orientalis*, the Chinese Arbor Vitæ.

In the sub-family *Cupressinæ*, including the genera Cupressus and Chamæcyparis, the ripe cone is woody and consists of 2–6 pairs of peltate macrosporophylls coherent by their margins in a valvate manner. The genus Cupressus, the Cypress, has several seeds on each macrosporophyll: in Chamæcyparis each macrosporophyll bears only two seeds.

The sub-family *Juniperinæ*, including the single genus Juniperus, is distinguished from the preceding sub-families in that the flowers are, as a rule, diœcious; the ripe cone is somewhat fleshy, resembling a berry or a drupe; it usually consists of one whorl of macrosporophylls each bearing one or two wingless seeds.

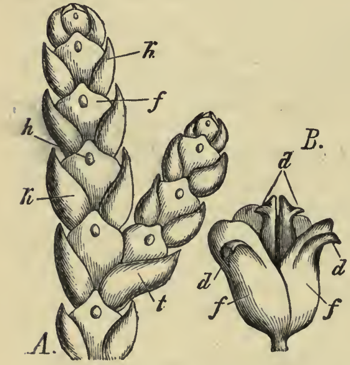

FIG. 306.—*A* Branch of *Thuja occidentalis* (×6) showing heterophylly; *k* flank-leaves; *f* surface-leaves; *h* resin-receptacle (see p. 464). *B* Fruit of *Biota orientalis* (nat. size): *f* macrosporophylls with ventral outgrowths *d*; *d* (in the middle line) sterile sporophylls.

The section Caryocedrus (Arceuthos), containing the single species *Juniperus drupacea*, has a cone consisting of 3 or 4 whorls of macrosporophylls; whereas in the section Oxycedrus (including *Juniperus communis*, the Juniper; *J. Oxycedrus*, *J. macrocarpa*, and other species), the cone consists of 1–2 whorls; and in the section Sabina (including *J. Sabina*, *J. virginiana*, etc.), it consists of 2–3 whorls; the innermost or uppermost whorl alone is fertile as a rule, in Caryocedrus and in Oxycedrus, but is sterile in Sabina: in Caryocedrus the (2–3) seeds are coherent, in the other two sections they are free: in Sabina the flowers are generally monœcious; in Sabina also the leaves (including sporophylls) are usually in whorls of 2, whilst in the other two sections they are in whorls of 3.

Sub-order II. **Taxoideæ**: the macrosporangiate flowers are, as a rule, not cones; the seed usually projects beyond the macrosporophylls (when present) and has a succulent testa or an arillus: flowers generally diœcious.

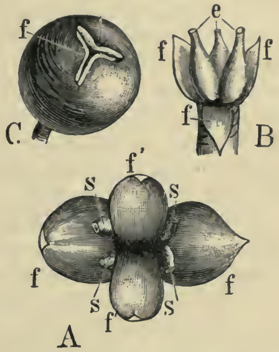

Fig. 307.— *A* Macrosporangiate flower of *Juniperus Sabina*, seen from above: *f f* fertile macrosporophylls, bearing macrosporangia *s*; *f'f'* upper part of sterile sporophylls (mag.). *B* and *C* *Juniperus communis*. *B* young fruit: *f f f* macrosporophylls, of which the anterior is turned down: *e* the ovules. *C* ripe fruit; the limits of the three carpels are only distinguishable at the apex.

Fam. 1. *Podocarpeæ*: the macrosporangiate flower consists of several macrosporophylls each bearing a single macrosporangium: the ripe seed is invested by an arillus: the microsporophylls each bear two microsporangia; the microspores have expansions of the exine.

This family includes the genera Saxegothea, Microcachrys, Podocarpus, and Dacrydium. Saxegothea resembles the Cupressineæ n that the macrosporophylls enclose the seeds: this genus is monœcious. On the other hand Dacrydium resembles the Taxeæ in that the macrosporophylls are very similar to the foliage-leaves, and in that the macrosporangia are sometimes borne in the axils of the macrosporophylls, and are then erect, whereas in all other cases they are inverted.

Fam. 2. *Taxeæ:* the macrosporophylls are usually rudimentary or absent, and the macrosporangia are borne on the axis: the seed has an arillus in some forms, while in others it has a succulent testa: microsporophylls with 2–9 microsporangia: microspores without expansions of the exine.

Phyllocladus, remarkable for its rudimentary leaves and for the development of its dwarf-shoots into phylloclades, has thick persistent macrosporophylls; in the axil of each there is a single erect macrosporangium with an arillus: flowers sometimes monœcious. *Ginkgo biloba* (*Salisburia adiantifolia*), the Maiden-Hair Tree, is characterised by its fan-shaped deciduous leaves with furcate venation: the macrosporophylls are rudimentary: the macrosporangia are borne in an opposite pair at the end of a short stalk: no arillus, but the testa of the seed becomes succulent. Cephalotaxus (the Chinese Yew) and the genera Taxus (the Yew) and Torreya (the Fetid Yew of North America) have only long shoots: the macrosporangiate flowers and the ripe seeds of Cephalotaxus resemble those of Gink-

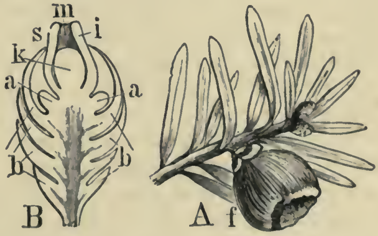

Fig. 308.—*A* Branch of *Taxus baccata* bearing a fruit *f*, which consists of a fleshy arillus enclosing a seed. *B* Longitudinal section of the end of a branch terminating in a macrosporangiate flower: *b* scaly bracts; *k* terminal macrosporangium (nucellus); *i* the integument; *m* the micropyle; *a* the rudiment of the arillus (×20).

go: in Torreya and Taxus (Fig. 308) there are no macrosporophylls, the macrosporangia being borne singly at the end of short lateral shoots, and the seed has a fleshy arillus. Taxus has no resin-ducts in its tissues: its microsporophyll is peltate, bearing 5–9 microsporangia on its under surface.

Order 3. **Gnetaceæ.** This order includes but three genera, Ephedra, Gnetum, and Welwitschia. Though they differ widely from each other in many respects, they agree in that they have opposite leaves; flowers which are not cones and which have a rudimentary perianth, but have no macrosporophylls as the macrosporangia are borne on the axis; an albuminous erect seed; a dicotyledonous embryo; and secondary wood which contains true vessels. They are generally diœcious.

The flowers are arranged in single or compound spicate inflorescences, arising either singly (Welwitschia) or in clusters from the axils of pairs of opposite and decussate bracts. The bracts are highly developed and closely packed in Welwitschia, so that the whole inflorescence has a somewhat cone-like appearance.

The perianth, in all cases uncoloured, consists of a single pair of coherent perianth-leaves, except in the microsporangiate flowers of Welwitschia, where there are two decussate pairs of free perianth-leaves.

The microsporangiate flower, in addition to the perianth, consists: in Ephedra, of a short projecting axis bearing 2–8 microsporophylls represented by sessile or shortly-stalked anthers each bearing two microsporangia; in Gnetum, of a short projecting axis directly bearing one or two microsporangia; in Welwitschia, of six monadelphous microsporophylls with well-developed filaments each bearing a terminal anther with three microsporangia, surrounding a rudimentary macrosporangium, with a projecting integument, in the centre of the flower.

The macrosporangiate flower, in addition to the perianth, consists: in all three genera of a terminal macrosporangium, borne on the axis; it is invested either by a single integument, as in Ephedra and Welwitschia, which is produced into a long projecting micropyle; or by two integuments (Gnetum) the inner of which forms a long projecting micropyle.

The fruit is formed: in Ephedra, by the succulent development of some of the bracts of the inflorescence which assume a red colour and enclose the fruitlets formed from the several flowers by the lignification of the perianth round the seed; in Gnetum, by the succulent development of the perianth and the lignification of the outer integument, in each separate flower; in Welwitschia, by the further development of the bracts, which assume a bright scarlet colour, and by the growth of the perianth around the seed so as to form a wing-like expansion, the winged seeds being set free by the falling to pieces of the cone-like inflorescence from below upwards.

Ephedra is a genus of shrubby plants, with rudimentary leaves, somewhat resembling an Equisetum. It is especially remarkable on account of its peculiar embryogeny (see p. 471). Habitat, warmer temperate zone.

Gnetum is a genus of shrubs or trees, for the most part climbers, but some erect-growing (*Gnetum Gnemon*): with its broad well-developed foliage-leaves, with pinnate venation, it resembles the Dicotyledons in habit. Habitat, the tropics.

Welwitschia includes the single species *W. mirabilis*: it is remarkable for its short thick stem, prolonged below into a tap-root, with a broad flat somewhat circular bilobed upper surface, a single long persistent foliage-leaf being borne at the margin of each lobe: the inflorescences are borne in dichotomous cymes, usually in the axil of each of the two leaves. Habitat, Damaraland, Western South Africa.

DIVISION B.

CLASS II.—ANGIOSPERMÆ.

The plants of this class are to a large extent herbaceous annuals, biennials, or perennials; but it also includes a great number of shrubs and trees.

THE SPOROPHYTE.

The General Morphology of the Vegetative Organs is so varied that it cannot be dealt with in a general way. The reader is referred to the treatment of the subject in Book I., and to the descriptions given in the systematic account of the class.

The General Morphology of the Reproductive Organs. The reproductive organs are *pollen-sacs* (microsporangia) and *ovules* (macrosporangia), borne generally on sporophylls, but sometimes directly on the floral axis (*e.g.* microsporangia of Naias, Casuarina, etc.; macrosporangia of Polygonum, Primulaceæ, etc.): they are developed in special shoots differentiated as *flowers*, and the flowers are arranged in a more or less complex branch-system, the *inflorescence*.

The Inflorescence (see p. 76). It is only in comparatively few cases that the primary axis of the plant terminates in a flower; such plants are said to *uniaxial*: it is usually not until the secondary or tertiary branches, or even those of a higher order, are developed, that a flower is formed. Such plants are said to be *bi-*, *tri-*, or *poly-axial.*

The floral axis of the Angiosperms frequently forms an elaborate branch-system which is usually sharply defined, as a sporophore, from the vegetative shoots, and which bears leaves which are either sporophylls or hypsophylls (p. 59).

In the inflorescence, as usually in all parts of the shoot of Angiosperms, the branching is almost always monopodial and axillary. Some apparent exceptions may be easily reduced to this type: thus, in the racemes of most of the Cruciferæ the bracts at the bases of the individual lateral branches are abortive, and the same occurs in many of the Compositæ. In the Solanaceæ and

Boraginaceæ the bract often undergoes displacement, so that it appears to be inserted laterally upon the axillary branch; on the other hand, it sometimes happens that the axillary branch is adherent to the main shoot for some distance.

The flowers of an inflorescence are either *sessile* or stalked, the stalk being termed a *pedicel.*

In accordance with the principles of branching laid down on p. 33, the different forms of inflorescences may be classified as follows :—

A. *Racemose Inflorescences* consist of a main axis (rhachis, peduncle), bearing a number of lateral branches developed in acropetal (or centripetal) succession, constituting a monopodial branch-system. The lateral branches do not usually grow longer than that portion of the main axis which lies above their points of origin. If the lateral shoots of the first order terminate in a flower without again branching, the inflorescence is said to be *simple*; but if they branch, it is *compound.*

These inflorescences are also termed *indefinite*, not because the apical growth of the main axis or of its branches is unlimited, but because, owing to the acropetal succession in the development of the flowers, the growth of branches of a high order is arrested, by the development of a terminal flower, earlier than that of branches of a lower order: for instance, the growth of the secondary branches is arrested before that of the main axis, that of the tertiary branches before that of the secondary branches, and so so.

I. *Simple racemose inflorescences :*

(α) *With an elongated main axis :* the lateral shoots spring from the axis at some distance from each other. The three following forms may be distinguished :

(1) The *spike*, in which the lateral branches are flowers which are sessile on the main axis, or have very short pedicels (Fig. 309 *A*); *e.g.* the inflorescence of the Plantain (Plantago). The small spikes of the Glumales are termed *spikelets.*

(2) The *spadix*, which differs from the spike only in having a thick and fleshy axis; a large bract forming a sheath, called a *spathe*, commonly grows at the base of the inflorescence and envelopes it more or less; *e.g.* Arum and Richardia.

(3) The *raceme*, in which the lateral branches are flowers with pedicels of nearly equal length, *e.g.* the Cruciferæ, as the Radish, Cabbage, etc.; in these the bracts of the individual flowers are not developed; also Berberis and others.

(β) *With a short main axis ;* the lateral branches are set closely together on the short or flattened main axis.

(4) The *capitulum* (head) in which the short main axis is conical or disc-shaped or even hollowed out, and is closely covered with lateral branches in the form of sessile flowers (Fig. 309 *D*), *e.g.* the Compositæ, as Dandelion, Sunflower; also the Scabious. The bracts (paleæ) of the individual flowers (Fig. 309 *D p*) are sometimes wanting; but the whole head is surrounded at the

base by a number of bracts forming an *involucre* (Fig. 309 *D i*) which gives the inflorescence the appearance of being one single flower.

(5) The *umbel*, composed of a number of lateral branches, in the form of pedicillate flowers, springing together from a very short axis which commonly terminates in a flower (Fig. 309 *C d*) ; *e.g.* the Umbelliferæ and the Ivy. The bracts of the separate pedicels forming *the rays* are usually present in diminished number ; they form an involucre.

II. *Compound racemose inflorescences* are formed when the lateral shoots which bear flowers, as described above, are again branched, or, in other words, when inflorescences of the types above enumerated are united to form a larger inflorescence ; for instance, when several capitula are arranged on the main axis in the same way as the flowers of a raceme. The same terms are applied to the first ramification of the compound inflorescence as to the simple ones described above ; the above-mentioned example, for instance, is a raceme of capitula, and is termed a capitulate raceme. Compound inflorescences may be classified as follows :

(α) *Homogeneously compound;* in these the branches of the first and second (or higher) orders are of the same character.

(6) The *compound spike* ; in this form many simple spikes are arranged on the main axis of the inflorescence in the same way as the flowers in a simple spike, or, in other words, the main axis of the spike bears secondary spikes instead of single flowers, *e.g.* the inflorescence of Wheat, Rye, etc.

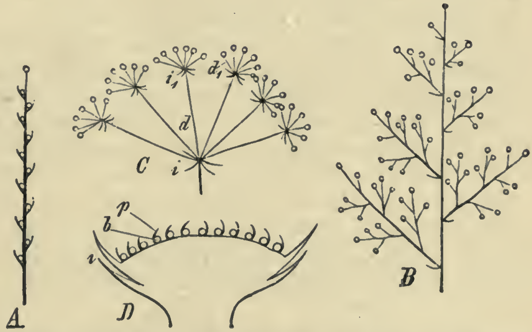

FIG. 309.—Diagrams of the varieties of racemose inflorescences. *A* Spike. *B* Compound raceme. *C* Compound umbel ; *d* rays of the umbel ; *i* involucre ; d_1 secondary rays of the umbellules ; i_1 involucel. *D* A capitulum ; *i* involucre ; *b* flower ; *p* bracts.

(7) The *compound raceme* ; in this case smaller racemes grow on the main axis of the raceme ; the ramification is in many cases still further repeated in such a way that it is more complex at the base of the primary raceme than towards the apex, *e.g.* the Grape-vine (Fig. 309 *B*).

(8) The *compound umbel* (Fig. 309 *C*). This is far more common than a simple umbel, and is in fact usually called an umbel ; the separate simple umbels (Fig. 309 C *d*) are then called *umbellules*, and their respective involucres are *involucels*.

(β) *Heterogeneously compound inflorescences;* in these the branches of the different orders are dissimilar. In consequence of this so many complicated forms arise that it is impossible to enumerate and name all the combinations. As examples, the following will only be mentioned : the *capitulate raceme*, which consists of a number of capitula arranged in a raceme; it occurs in many of the Compositæ, *e.g.* Petasites: the *spicate capitulum*, which consists of several spikes forming a capitulum, as in the Scirpoideæ: the *spicate raceme*, which occurs in many Grasses, in which the last branches of a compound raceme are spikes.

B. *Cymose Inflorescences:* the main axis produces one, two, or more lateral branches—rarely several—at the same level below its apex, which grow more vigorously than the main axis, and repeat the same type of branching.

These inflorescences are also termed *definite* because the growth of each axis is arrested, by the development of a terminal flower, before that of the lateral branch or branches which it bears. The simplest kind of definite inflorescence is that in which the axis (peduncle) does not branch, but bears a single terminal flower.

Cymose inflorescences are also termed *centrifugal*, because the development and expansion of the flowers begins with the primary axis, and occurs successively in the axes of the second, third, and higher orders.

I. In the *simple cyme* the ramification in the secondary and higher orders follows the same type.

(α) *Without a pseud-axis* (see page 35).

The *cyme*: beneath the terminal flower spring several—three or more—lateral shoots of equal vigour, *e.g.* many Euphorbiæ. This inflorescence greatly resembles the true umbel, and in fact cannot be distinguished from a true umbel which has a terminal flower. The identification of an inflorescence as belonging to the cymose type depends in many cases on the fact that in the higher orders of branching the cymes are reduced to dichasia.

The *dichasium* (Figs. 19 *C* and 20) consists of only two equal lateral shoots arising at the same level below the terminal flower, and branching in a similar manner. The successive false dichotomies commonly decussate, *e.g.* Valerianella and the weaker inflorescences of many Euphorbiæ.

(β) *With a pseud-axis.*

The *scorpioid cyme* (cincinnus and rhipidium): in this the lateral branches occur alternately on opposite sides (Fig. 19 *A* and *B*): Boraginaceæ, Crassulaceæ, Iridaceæ, Commelynaceæ, etc.

The *helicoid cyme* (bostryx and drepanium): the lateral branches of the successive ramifications always occur on the same side (Fig. 19 *D*): this is frequently found in Monocotyledons, such as Hemerocallis, Ornithogalum, Alstrœmeria, Juncaceæ.

It has been ascertained, however, that in many cases (various Solanaceæ and Boraginaceæ) the so-called scorpioid cymes are monopodial; the axis is therefore not a pseud-axis but a true one, and the inflorescence must be regarded as a unilateral raceme.

II. *Compound cymose inflorescences* arise on the one hand from the reduction of the ramification in the higher orders, as, for instance, when the secondary members of a cyme are not cymes, but dichasia: these are *dichasial cymes*; they occur in many Euphorbiæ: again, when dichasia terminate in scorpioid or helicoid cymes. On the other hand it sometimes occurs that helicoid cymes are combined to form scorpioid cymes, as in Geranium.

C. *Compound racemose and cymose inflorescences.* It may occur that a compound inflorescence changes in type in the different orders of ramification. Thus the branches of the first order may exhibit a racemose arrangement, and those of the second a cymose arrangement, as in the dichasial racemes of many Euphorbiæ (*e.g. E. Esula*, *amygdaloides*), in the scorpioid racemes of the Horse-chestnut, and in the helicoid capitula of many species of Allium. On the other hand the branches of the first order may have a cymose, and those of the second a racemose arrangement; for instance, the helicoid cymes of capitula in Cichorium.

Finally, there are certain terms used in describing inflorescences which refer only to the general external appearance rather than to the mode of formation of the inflorescence : thus, the *panicle* is a pyramidal inflorescence generally of the racemose type, at least in its first ramification : the *corymb* is a racemose inflorescence of which all the ultimate ramifications lie in one plane and bear flowers, *e.g.* the Elder, many Cruciferæ : the *amentum* (catkin) is a simple or compound spicate inflorescence, usually pendulous and elongated, bearing inconspicuous monosporangiate flowers, which falls off entire from the plant when the flowering is over. Of cymose inflorescences there is the *fascicle*, consisting of a number of flowers on pedicels of equal length (Sweet William) ; the *glomerule* (Nettle and Box) or *verticillaster* (many Labiatæ), consisting of a few sessile or shortly pedicillate flowers ; and the *anthela*, which is a compound inflorescence, in which the branches of the first order are gradually shorter from below upwards (or rather from without inwards), as in Juncaceæ.

To a floral axis arising from the ground, with no leaves, or with only a few bracts, bearing a single flower or a more or less complex inflorescence, the term *scape* is applied.

The *Bracts* (p. 79) are leaves borne on the inflorescence, in the axils of which the flowers are developed : there may be a single large bract, termed a *spathe*, enclosing the whole inflorescence, as in palms and in the Arum Lily (*Zantedeschia æthiopica*) where the bract is white ; or the bracts may be brightly coloured (petaloid), as in Poinsettia and other Euphorbiaceæ where they are red, and in *Leycesteria formosa*, *Melampyrum*, etc. ; or the bracts may be scaly, forming an *involucre* round the inflorescence as in the Compositæ : the *glumes* of the Grasses are scaly bracts ; the bracts are frequently not very unlike the foliage-leaves, differing from them mainly in form and size.

The portion of the floral axis below the flower (*i.e.* the peduncle or the pedicel) commonly bears one or more *bracteoles* or *prophylla*. In most Monocotyledons there is a single posterior prophyllum, whilst in most Dicotyledons there are two lateral prophylla. In some Monocotyledons, however (*e.g.* Hydrocharidaceæ, such as Elodea, Vallisneria, Halophila ; and Amaryllidaceæ, such as Galanthus, Narcissus, Leucojum, etc.), there are two lateral prophylla (remaining free in Hæmanthus) which unite to form the so-called spathe which invests the flower of these plants. On the other hand, some Dicotyledons have a single prophyllum which is, however, always lateral: this is frequently the result of the suppression of the second prophyllum, but there are cases (*Ranunculus aquatilis*, *auricomus*, *Lingua*) in which this is apparently the normal condition.

In some cases several bracteoles are arranged in a whorl, forming an *epicalyx*, either close beneath the flower (as in Malva, *Anemone Hepatica*, Dipsacus, Clusia, Camellia), or at some distance below it (other species of Anemone). In some Nyctaginaceæ the epicalyx may become an involucre enclosing several flowers; this is due to the fact that flowers are developed in the axils of some of the bracteoles of the terminal flower. Though they are generally green, the bracteoles are sometimes brightly coloured, as in some Amarantaceæ and Nyctaginaceæ; or scaly, as the lodicules of Grasses.

The *Flower* (p. 76) consists of an axis bearing, as a rule, both perianth-leaves and sporophylls on the somewhat shortened and expanded terminal portion of the axis which is the *receptacle* or *torus*.

The perianth-leaves are generally differentiated into two series: an outer, of usually rather small green leaves, the *sepals*, constituting the *calyx*: an inner, of usually conspicuous brightly coloured leaves, the *petals*, constituting the *corolla*.

The flower is usually ambisporangiate (hermaphrodite, monoclinous), but is not infrequently monosporangiate (unisexual, diclinous, or even diœcious). The sporangia, with but few exceptions, are borne upon sporophylls (see p. 78): the microsporophylls (stamens) constitute the *andrœcium*, the macrosporophylls the *gynœceum*, of the flower.

The growth of the floral axis terminates with the development of the floral leaves at its apex, excepting in abnormal cases; and buds are not developed, except in monstrosities, in the axils of these leaves. The characteristic feature of that portion of the floral axis which actually bears the flower is that the internodes between successive floral leaves or whorls of leaves, are not as a rule developed, so that all the floral leaves are closely packed and are nearly at the same level, the perianth-leaves being external and the sporophylls internal. It occasionally happens, however, that one or more of the internodes within the flower may be developed to some extent: for instance, the internode (termed *anthophore*) between the calyx and the corolla, as in Lychnis and some other Caryophyllaceæ; that (termed *gonophore*) between the corolla and the andrœcium, as in the Passion-Flower, and in Orchids where the styles adhere to it forming the *gynostemium* or *column*; that (termed *gynophore*) between the andrœcium and the gynæceum, as in Cleome (Capparidaceæ), some Gentians, and some Cruciferæ: in Gynandropsis (Capparidaceæ) two internodes are developed, a gonophore and a gynophore.

When the axis grows, as is usually the case, equally in all parts, the gynæceum, being nearest to its apex, is the uppermost part of the flower. When this is the case its insertion is above that of the andrœcium and perianth (Fig. 310 *H*), and the ovary is said to be *superior* and the flower *hypogynous*, as in Ranunculus, Papaver, Lilium, and Primula. But in a great number of plants the perianth and andrœcium are raised by the intercalary growth (see p. 17) of a lower portion of the axis (as represented by the outer portion of the torus) and stand on a circular rim surrounding the apex of the axis which lies at a lower level. Of this condition two different forms occur:—in the one, the carpels are inserted in the depression at the apex of the axis (Fig. 310 *P*), and there form one or more ovaries free from it, primarily at least, though they may subsequently become adherent to it; in such cases, as in the Rose and Apple, the flower is said to be *perigynous*: in the other, the carpels spring from the upper rim of the cavity which is formed by the axis itself and simply cover it in at the top; such flowers are said to be *epigynous*, and the ovary to be *inferior*, *e.g.* Gourds and Umbelliferæ (Fig. 310 *E*). Many transitional forms between these two extremes are found.

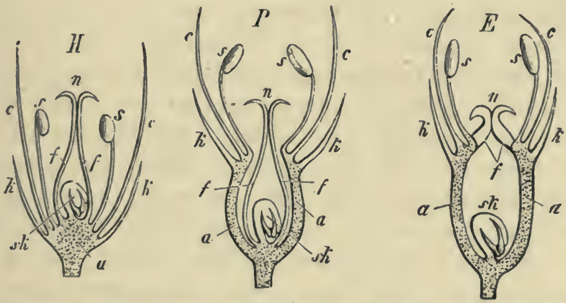

FIG. 310.—Diagram of *H* hypogynous; *P* perigynous; *E* epigynous flowers; *a* axis; *k* calyx; *c* corolla; *s* stamens; *f* carpels; *n* stigma; *sk* ovule.

Stipules are sometimes developed in connection with the floral leaves; thus in some Rosaceæ (Potentilla, Comarum, Geum, Alchemilla) the stipules of the sepals form a *calyculus* or *epicalyx*: stipules are developed in connexion with the petals of some Sapotaceæ (Dipholis, Mimusops); and in connexion with the stamens of Allium, Ornithogalum, some Zygophyllaceæ, etc.

The Phyllotaxy of the Flower. The floral leaves, like the foliage-leaves on the stem (see p. 25), are frequently arranged spirally, (*e.g.* Calycanthus, Anemone, Trollius) when the flower is *acyclic.* The most common divergence is $\frac{2}{5}$, but higher divergences also occur, especially in the andrœcium, when numerous small organs are inserted upon an expanded axis (*e.g.* Ranunculus). In the spiral or acyclic flower there is either no well-marked distinction of the various series, that is, the members of the calyx, corolla, and andrœcium, are connected by intermediate forms (*e.g.* Nymphæa); or the various series are sharply defined, each series taking up one or more turns of the spiral.

In most cases the floral leaves are arranged in whorls, that is, the flowers are *cyclic.* Cyclic flowers are connected by intermediate forms with the acyclic, especially through pentamerous forms. Thus some pentamerous flowers are *hemicyclic*, that is, some of their floral leaves are arranged spirally, and the others in whorls. Instances of a spiral perianth combined with cyclic sporophylls are afforded by those flowers in which the members of the perianth, calyx, or corolla are developed in $\frac{2}{5}$ succession, and the prefloration is quincuncial (see p. 60); the perianth is spiral in the flowers of the Cannabinaceæ, Chenopodiaceæ, and Amarantaceæ; the calyx is spiral in the flowers of the Bindweed (*Calystegia Sepium*), the Rose, some Boraginaceæ (Cerinthe, Echium, etc.), Geraniaceæ, Oxalidaceæ, Linaceæ, Caryophyllaceæ, and many other dicotyledonous orders; both calyx and corolla are spiral in Ternstrœmia and Clusia. Though the phyllotaxy is not $\frac{2}{5}$ in Camellia, the calyx and corolla are spirally arranged. In other cases, the sporophylls are spirally arranged, whilst the perianth-leaves are cyclic. For instance, in Magnolia, Ranunculus, and Helleborus, both stamens and carpels are spirally arranged; and in Delphinium and Aconitum, the stamens only.

Closely related to the foregoing cases of $\frac{2}{5}$ phyllotaxy—occurring in fact not only in flowers of closely allied species, but also in flowers of the same species—are certain of the typical forms of cyclic arrangement in which each series (whether perianth, calyx, corolla, or andrœcium), instead of consisting of five floral leaves, taking up two turns of a spiral with a divergence of $\frac{2}{5}$, consists of four or six leaves arranged in two whorls, consisting respectively of two or three leaves.

For purposes of comparative description, it is convenient to regard each turn of the spiral in an acyclic or a hemicyclic flower as equivalent to a whorl: thus a well-defined series with $\frac{2}{5}$ arrangement would represent two whorls.

As in the case of the foliage-leaves (see p. 45), so in that of the floral leaves, the order of development is as a rule acropetal: hence each whorl of the flower is developed later than the one external to it, and earlier than the one internal to it. When, however, a series of floral organs is becoming degenerate, its development is retarded; for instance, in the Compositæ, Valerianaceæ, and Umbelliferæ, the degenerate calyx is developed after the corolla, or even after the andrœcium. The members of each whorl may be developed either simultaneously or successively.

In their arrangement, also, the floral leaves resemble the foliage-leaves. When, in an acyclic or hemicyclic flower, the spiral is continuous with the same divergence from one series of floral organs to another, the members of the successive series lie on the same radii drawn from the centre of the flower, that is, they are *directly superposed*. A good example of this is afforded by the terminal flower of the inflorescence of Berberis (Fig. 311; occasionally in Epimedium, and also in Gagea among Monocotyledons), where the stamens, petals, and sepals are all directly superposed: similarly in Ternstrœmia and Clusia, where the sepals and petals are in a continuous $\frac{2}{5}$ spiral, the petals are superposed on the sepals. When, on the other hand, the divergence varies from one series to another, direct superposition does not occur, but some form of alternation, as is generally the case in acyclic flowers: for instance, the calyx of certain (pentamerous) forms of Anemone and other Ranunculaceæ is arranged with a $\frac{2}{5}$ divergence, whereas the divergence of the stamens is $\frac{5}{13}$ or $\frac{8}{21}$. In hemicyclic flowers with a simple spiral perianth and cyclic stamens (*e.g.* Cannabinaceæ, Chenopodiaceæ, Amarantaceæ), the stamens are superposed on the perianth-leaves.

When the floral leaves are in whorls consisting of equal numbers of members, the general rule is that the members of the successive whorls alternate with each other: thus, in a flower with calyx, corolla, andrœcium, and gynæceum, each consisting of a single whorl of five members, the petals alternate with the sepals, the stamens with the petals, and the carpels with the stamens; and if radii be drawn from the centre of the flower, it will be seen that the stamens are opposite to the sepals and the carpels to the petals, or more briefly, that the stamens are *antisepalous* and the carpels are *antipetalous.* This is not, however, a case of direct superposition, since the corolla intervenes between the andrœcium and the calyx, and the andrœcium intervenes between the gynæceum and the corolla.

There are, however, certain cases in which this law of alternation does not prevail, in which, that is, the members of successive whorls are *directly* superposed. For instance, the (4–5) stamens are directly antipetalous in several natural orders (Primulaceæ, Myrsinaceæ, Sapotaceæ, Plumbaginaceæ, Ampelidaceæ, Rhamnaceæ); again, in some Campanulaceæ (*e.g. Campanula Medium*, Fig. 312, Michauxia) the (5) carpels are directly superposed on the stamens.

The Floral Diagram.—These various arrangements of the floral leaves, like those of the foliage-leaves, are most clearly represented by means of diagrams (see p. 25). In a *floral diagram*, the calyx lies externally, and the gynæceum, as being the uppermost series of organs (even in epigynous flowers) lies most internally. In order to be able readily to distinguish the various series, symbols are used which recall some peculiarity of their form: thus the midrib of the sepals is indicated, and, in the case of the stamens, the anthers.

FIG. 311.—Floral diagram (ground-plan) of an acyclic flower, with $\frac{2}{5}$ divergence in the calyx, corolla, and andrœcium (terminal flower of Berberis: after Eichler).

FIG. 312.—Floral diagram of *Campanula Medium*: the five carpels are directly superposed on the stamens. (After Eichler).

If only such relations of position as can be actually observed in a flower are indicated in the diagram, a simple *empirical diagram* is the result. If, however, the results of the investigation of the development of the flower and of the comparison of it with others be borne in mind, a general plan of arrangement will be detected, and the individual peculiarities of arrangement, quite apart from any variation in the form of the organs, will be seen to be due either to the suppression of one or more whorls or of one or more members of a whorl, or, more rarely, to a multiplication of the whorls or of their members. If, however, the organs which are absent, but which should typically be present, be indicated in the empirical diagram by dots, it becomes a *theoretical diagram*. In this way it is possible to arrive at general types on which large numbers of flowers are constructed. Fig. 313, for instance, is the empirical diagram of the flower of the Lily, and it is at the same time the type on which the flower of Grasses (Fig. 314) is constructed in which certain organs are suppressed.

In constructing a floral diagram the position of the main axis should be indicated by a dot placed above the diagram: the bract, which would of course be exactly opposite to it, may or may not be indicated: the side of the flower toward the main axis is said to be *posterior*, and that toward the subtending bract, *anterior*. A plane which passes through the flower and also through the main stem and the median line of the bract is termed the *median plane* or *section* of the flower: the plane which cuts the median plane at right angles is the *lateral plane* or *section*: and the plane which bisects the angles made by the intersection of the median and lateral planes is the *diagonal plane* or *section*: any plane other than these is said to be *oblique*. By means of these conceptions the position of the parts of a flower may be accurately indicated: thus, in describing the flower of the Cruciferæ (Fig. 315), the two external sepals lie in the median plane; the two inner sepals, the two outer stamens, and the two carpels, in the

FIG. 313.—Floral Diagram of a Lily.

FIG. 314.—Floral Diagram of a Grass.

FIG. 315.—Floral Diagram of a Crucifer; the median stamens are duplicated.

lateral plane; whilst the petals and the four inner stamens lie in the diagonal planes.

The number and the relations of the different parts of the flower may be indicated not by diagrams only, but also by formulæ in which, as in the diagrams, for the sake of clearness, all the peculiarities of form are overlooked. Thus the diagram Fig. 313 may be expressed by the formula $K3$, $C3$, $A3 + 3$, $G^{\underline{(3)}}$, which means that the calyx K, and the corolla C, each consist of a single whorl of three members, the andrœcium of two whorls each of three members, and the gynæceum of one whorl of three members, all in regular alternation. When one whorl is superposed on another, the superposition is indicated in the formula by a line $|$ between the whorls. If the number of members in any whorl is variable, the letter n is used instead of a number. Thus, for instance, $K\mathrm{n}$, $C\mathrm{n}$, $A\mathrm{n} + \mathrm{n}$, $G\mathrm{n}$ is the theoretical formula of most Monocotyledons. The absence of a whorl is expressed by a cypher 0, and of individual members by the number of those actually present. Thus the formula for the flower of a Grass (Fig. 314) is $K0$, $C0$, $A3 + 0$, G^{1}. Superior and inferior ovaries are indicated by a stroke below or above the corresponding figure, and duplication by the exponent 2; thus the diagram Fig. 315 is represented by the formula $K2 + 2$, $C \times 4$, $A2 + 2^2$, $G^{\underline{(2)}}$, the × after C indicating that the position of the petals is diagonal, *i.e.* that the four petals alternate with the four sepals, as if the latter all belonged to the same whorl. The bracket in which the number of the carpels of the gynæceum G is enclosed, indicates that the members thus bracketed are coherent. Staminodia may be distinguished by a † before the figure. When the perianth is not differentiated into calyx and corolla, it is expressed by the letter P: thus the formula for the flower of Chenopodium is $P5 \mid A5\ G^{\underline{(2)}}$.

The Number of Members in a Whorl shows considerable variation: thus, in Monocotyledons it is generally three (rarely two or five), whereas in Dicotyledons it is frequently five, less frequently two or four, rarely three (*e.g.* most Lauraceæ, Berberis, Rheum, Polygonum). The number of members in a whorl is indicated by the terms *di- tri- tetra- penta-merous*, etc. Whorls containing the same number of members are said to be *isomerous*; or, when the number of members is not uniform, *heteromerous*. Flowers having isomerous whorls are said to be *eucyclic* or *isocyclic*, whereas when the whorls are heteromerous the flowers are said to be *heterocyclic*. Of these two conditions the latter is the more common, though the former is frequently realized (*e.g.* many Monocotyledons). The heterocyclic condition is due either to the number of members in one or more of the whorls being smaller (*oligomery*) or greater (*pleiomery*) than that which is the typical number. The commoner cases of oligomery are to be found in the whorls of sporophylls, especially in the gynæceum: for instance, the typically pentamerous flower of the Saxifragaceæ is heterocyclic because of the oligomerous (dimerous) gynæceum; similarly, in the Scrophulariaceæ, the andrœcium is generally, and the gynæceum is always, oligomerous, the former consisting of but two or four stamens, the latter of but two carpels. Pleiomery is of less frequent occurrence: however in the Cruciferæ (Fig. 315) the whorls of the calyx, the outer whorl of stamens, and the gynæceum, are dimerous, but the corolla and the inner whorl of stamens are tetramerous and hence pleiomerous: similarly, one or more whorls of the andrœcium in the Papaveraceæ, Phytolaccaceæ, and Polygonaceæ, are pleiomerous: and probably in other cases where the number of the stamens is twice that of the petals or sepals, that is, where the flower is *diplostemonous*, the condition is due rather to pleiomery (*duplication*) of a single whorl than to the development of two whorls as is usually assumed (see below, under pleiotaxy). Pleiomery of the corolla is common in double flowers.

Heteromery necessarily affects the alternation of the floral leaves of the successive whorls. Thus, in the Cruciferæ, where the calyx consists of two alternating dimerous whorls, and the corolla of a single tetramerous whorl, the four petals alternate with the four sepals just as if the sepals all belonged to a single whorl. When, as is very frequently the case, the gynæceum is oligomerous, the carpels (or carpel) present do not appear to occupy any definite position with regard to the preceding organs.

The Number of Whorls in the Flower. The simplest case is that in which each series of floral organs—calyx, corolla, andrœcium, gynæceum—occupies a single whorl, or is *monocyclic*: this is realised in a few natural orders, either accompanied with regular alternation (*e.g.* Asclepias, Cornus, Caprifoliaceæ generally, Iridaceæ, Orchidaceæ), or with antipetalous stamens (*e.g.* Rhamnaceæ, Ampelidaceæ). In this case the flower is *tetracyclic*.

More commonly one or more of the series may occupy two whorls, or be *dicyclic*. This is generally the case when the whorls are dimerous (*e.g.* both corolla and andrœcium of Oleaceæ and Fumariaceæ: corolla of Papaver: calyx and andrœcium of Cruciferæ; perianth of Urtica and Morus). Where the whorls are trimerous the dicyclic condition is frequent: thus in the majority of Monocotyledons there are two whorls of stamens whilst all the other series of the flower are monocyclic, so that the flower is diplostemonous with regular alternation: in the comparatively few trimerous flowers of Dicotyledons the dicyclic condition may be observed in the andrœcium (Rheum, Polygonum, Berberis), or in calyx, corolla, and andrœcium (Cocculus). The $\frac{2}{5}$ calyx, which is to be found in very many Dicotyledons, may be regarded as equivalent to a dicyclic calyx (see p. 497). A dicyclic gynæceum is to be found in a few Monocotyledons (*e.g.* Alisma, Butomus) and Dicotyledons (Phytolacca, and Malvaceæ such as Malva, Althæa, Lavatera).

The conclusion to be drawn from these facts is that in the complete dichlamydeous ambisporangiate flowers of Angiosperms there are, as a general rule, five whorls of floral leaves; the flowers are *pentacyclic*. In most Monocotyledons the five whorls belong, one to the calyx, one to the corolla, two to the andrœcium, and one to the gynæceum: in most Dicotyledons they belong, two to the calyx, one to the corolla, one to the andrœcium, and one to the gynæceum.

If, now, such a pentacyclic flower with regularly alternating whorls be taken as a type or standard of comparison, it will be observed that many flowers deviate from it by having either a larger or a smaller number of whorls, the deviation being combined in some cases with direct superposition.

Pleiotaxy, or an increase in the number of the whorls in a flower, is characteristic of a number of genera belonging to various natural orders. Instances have been mentioned above of Monocotyledons and of Dicotyledons having flowers with a dicyclic gynæceum; of Dicotyledons with a dicyclic corolla or andrœcium: but the number of whorls is sometimes much greater (15 in Aquilegia), when the flowers, as also the special series, are said to be *polycyclic*. Thus, the calyx is polycyclic in Nandina (Berberidaceæ) and in Sychnosepalum (Menispermaceæ); the andrœcium, in Aquilegia, Camellia, Rosa, Lauraceæ, and Papaveraceæ; the gynæceum, in some Alismaceæ and Butomaceæ. In some cases, one series becomes polycyclic at the expense of another: thus in the acyclic flowers of Clematis, Anemone, and Caltha, the petals are replaced by stamens so that the number of turns of the spiral (=whorls) in the andrœcium is increased whilst the corolla disappears. The "doubling" of flowers is commonly due to the polycyclic development of the corolla, the additional whorls being either new formations, or the result of the more or less complete replacement of the sporophylls by petals.

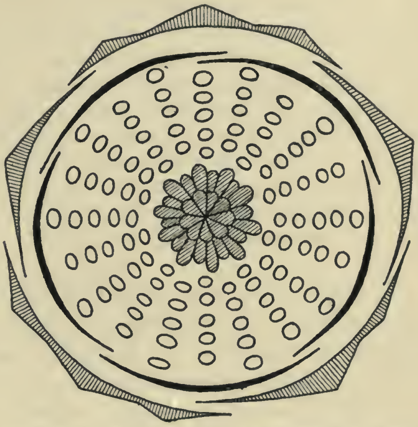

FIG. 316.—Floral diagram of *Rosa tomentosa*, showing the polycyclic andrœcium and gynæceum. (After Eichler.)

An important case is that to be found in several Dicotyledonous orders (Ericaceæ, Rhodoraceæ, Pyrolaceæ, Crassulaceæ, Fig. 318, Saxifragaceæ, some Caryophyllaceæ, Fig. 317; Onagraceæ, Fig. 323; Geraniaceæ, Oxalidaceæ, Zygophyllaceæ, Rutaceæ, Fig. 317 *C*) where the flower is diplostemonous, and the andrœcium is apparently dicyclic: but the flower is not simply diplostemonous (as in the Monocotyledons), because the whorls do not alternate regularly; the stamens of the apparently outer whorl are directly antipetalous, consequently the stamens of the inner whorl are antisepalous, and the carpels (in eucyclic flowers) are antipetalous. Such flowers are said to be *obdiplostemonous* (Fig. 317 *C*).

A variation of the typical obdiplostemonous flower is found in certain Caryophyllaceæ (*e.g.* Viscaria, Fig. 317 *A* ; Lychnis, Cerastium, some species of

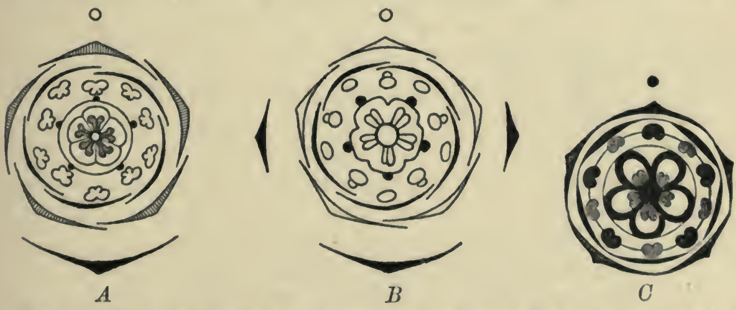

FIG. 317.—Floral diagrams of two Caryophyllaceous flowers illustrating two forms of obdiplostemony : *A* (*Viscaria vulgaris*) with antisepalous carpels : *B* (*Spergula arvensis*) with antipetalous carpels (after Eichler : *C* diagram of obdiplostemonous flower of Dictamnus.

Silene) with eucyclic (tetra- or penta-merous) flowers, in that, though the apparently outer stamens are directly antipetalous, the carpels are antisepalous. This case seems to be connected with that of the Primulaceæ (see p. 498), where there is a single whorl of antipetalous stamens and the carpels are antisepalous, through the Sapotaceæ where a whorl of antisepalous staminodes (Sideroxylon, Lucuma) or of fertile stamens (Isonandra) is developed. It would, in fact, appear that obdiplostemony may be the result of either pleiomery or pleiotaxy taking place in a primitively isomerous monocyclic antipetalous andrœcium (as in Primula); when the carpels, in an obdiplostemonous flower, are antisepalous, it seems to be simply a case of pleiomery; when they are antipetalous, it would seem to be a case of pleiotaxy, the andrœcium having become dicyclic by the development of an inner whorl of stamens consequently involving a change in the position of the gynæceum.

Oligotaxy, or a decrease in the number of whorls in a flower, is frequently due to *suppression*. For instance, owing to the suppression of one whorl of stamens in some Monocotyledons, either the outer (some Hæmadoraceæ, also Cypripedium), or the inner (Iridaceæ, most Orchidaceæ), the andrœcium is monocyclic. In some cases a whole series is suppressed: for instance the corolla may be absent (*e.g.* Glaux, among the Primulaceæ; Alchemilla, Sanguisorba, among the Rosaceæ: some Caryophyllaceæ, such as *Sagina apetala*, Scleranthus, etc.): or the andrœcium or gynæceum (monoclinous flowers, such as those of *Sedum Rhodiola*, *Rhamnus cathartica*, Hydrocharidaceæ, ray-florets of Compositæ, etc.): or the whole perianth (*Fraxinus excelsior*).

In most cases of oligotaxy in isomerous flowers, the relative position of the remaining whorls is undisturbed: thus, in the apetalous flower of Glaux, the typically antipetalous stamens alternate with the sepals, and in that of Sanguisorba the stamens are opposite to the sepals; in the carpellary flower of Rhamnus the carpels are antisepalous as in an ambisporangiate flower. But this is by no means always the case: for instance, in the apetalous flower of Alchemilla the stamens alternate with the sepals, seeming to take the place of the missing petals: again, the staminate flower of *Sedum Rhodiola* (Fig. 318) has rudimentary carpels which are antipetalous, whereas in the carpellary flowers the carpels are antisepalous, apparently occupying the place of one of the missing staminal whorls; similarly in Halophila (Hydrocharidaceæ) the three carpels of the carpellary flower occupy the same relative position as the three stamens in the staminate flower.

Although it is true that, as explained in the foregoing paragraphs, both oligotaxy and oligomery are frequently due to *suppression*, in the one case of one or more whorls, in the other of one or more members of a whorl, it must not be assumed that this is the only possible explanation. On the contrary, it is very probable that the simple structure of the flower in some plants (*e.g.* Urticales and Amentales among Dicotyledons) is not the result of suppression, but is itself typical: in other words, these flowers are probably to be regarded, not as *reduced*, but as *primitive*, belonging to plants which are, it may be, of a relatively low type among Phanerogams, but which are on the *up-grade*, and not on the *down-grade* of organisation. The distinction of primitive from reduced forms is, at the present time, perhaps the most important morphological problem presented by Angiosperms, for until it is solved the classification of the group will continue to remain unsatisfactory and inconclusive.

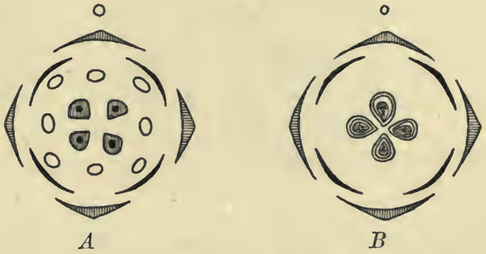

Fig. 318.—Floral diagrams of *Sedum Rhodiola*. In the staminate flower *A*, the (abortive) carpels are antipetalous: in the carpellary flower *B*, the carpels are antisepalous. (After Eichler.)

The Relations of Position between the floral leaves and those which precede them on the floral axis, can be most readily made out in the case of a flower borne laterally on a main axis, the pedicel springing from the axil of a bract. Where, as in most Monocotyledons, the flower-stalk bears but a single bracteole or prophyllum (see p. 493), this is generally situated opposite to the bract (Fig. 319 *A*), that is, posteriorly to the flower; in this case the odd sepal of the trimerous calyx is situated anteriorly. When, as in most Dicotyledons, there are two lateral prophylla (usually indicated as *a* and *β*), one on each side of the flower-stalk, the position of the sepals varies according to the

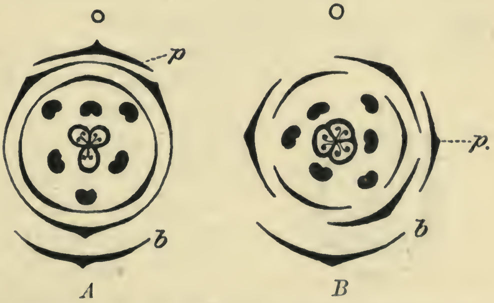

Fig. 319.—Floral diagrams of *Lilium bulbiferum* (after Eichler): A with normal position of the prophyllum p, opposite to the bract b: B with lateral prophyllum (p).

composition of the calyx: thus, if the calyx be trimerous or pentamerous, the odd sepal is, as a rule, median, generally posterior or, less commonly, anterior (*e.g.* Leguminosæ): the tetramerous calyx has usually two sepals in the median plane and two in the lateral (*e.g.* Philadelphus; Isnardia among Onagraceæ; *Rhamnus cathartica*, Ilex). In some few cases, when there are two lateral prophylla, the four sepals of an apparently tetramerous calyx are arranged diagonally (*e.g.* Veronica and other Scrophulariaceæ, Plantago, probably also Mimosa, Fig. 321); this exceptional position is due to the fact that in these plants the calyx is typically pentamerous, though, in consequence of the suppression of the posterior median sepal, it appears to be tetramerous.

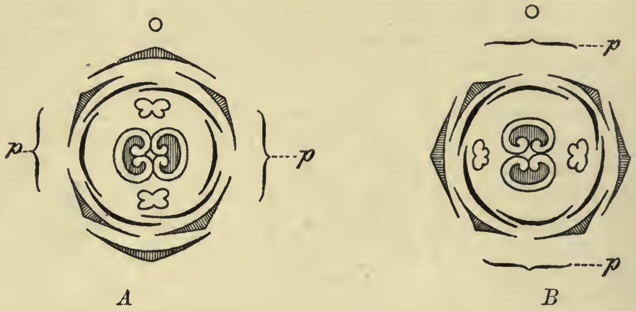

Fig. 320.—Floral diagrams of *Jasminum nudiflorum* (after Eichler): *A* with normal lateral position of the prophylla: *B* with antero-posterior position of the prophylla: the calyx is hexamerous and dicyclic, the two sepals of the outer whorl alternating with the prophylla: the symmetry of the flower is isobilateral.

As a general rule, the genetic relation between the sepals and the prophylla is that the first sepal of a successively-developed calyx arises on the opposite side of the axis (though higher) to the single prophyllum or to the upper (β) when there are two. Hence the position of the prophylla affects that of the sepals and, consequently, that of all the floral organs. Thus, it is not uncommon in the Monocotyledons for the single prophyllum to be placed either obliquely or laterally (some Liliaceæ, Canna, etc.), and then all the whorls of the flower present a corresponding displacement (Fig. 319 *B*); the same thing occurs

Fig. 321.—Floral diagram of Mimosa, showing the diagonal position of the sepals (after Eichler).

in Dicotyledons when, as is frequently the case, the prophylla are not exactly lateral, but converge anteriorly or posteriorly, or are even anterior and posterior (Fig. 320 *B*).

When the one or the two prophylla are suppressed, the position of the sepals may be the same as if the prophylla were present (*e.g.* Cruciferæ); but, more commonly, the first sepals are developed in the places of the missing prophylla. Thus, in the absence of two lateral prophylla, the first two sepals of a tetramerous calyx are lateral (*e.g.* tetramerous calyx of Francoa, Epilobium, Clarkia); again, in a trimerous calyx, the first normally anterior sepal tends to be posterior when the single posterior prophyllum is absent (*e.g.* Orchis, Musa); and, further, in a pentamerous calyx the first and second sepals are postero-lateral (*e.g.* Primula, Reseda) since the first sepal occupies the place of prophyllum α, and the second that of prophyllum β, with slight posterior convergence.

The Symmetry of the Flower. The flower presents all the varieties of symmetry which are discussed in Part I. (p. 8); these are mainly determined by the number and the relative development of the floral leaves, and in a few cases by the development of the floral axis or receptacle.

The symmetry may be *radial* or *actinomorphic.* When an eucyclic flower is also *regular*, that is, when the members of each whorl are similar to each other in size and form, it can be divided into symmetrical halves by sections made in two or more planes, the halves produced by section in one plane being similar to those produced by section in one or more other planes. Such a flower is *polysymmetrical* (see p. 9). The number of these *planes of symmetry* depends upon the numerical constitution of the flower. Thus a regular eucyclic trimerous flower (*e.g.* Lilium and other Monocotyledons) can be so divided in three planes, the median and the two diagonals, that all the three pairs of resulting halves are exactly alike (Fig. 322 *B*). Similarly, the pentamerous flower of Primula, Geranium, species of Campanula, is divisible in five planes (Fig. 322 *A*). But where the flower is tetramerous (*e.g.* Fuchsia, *Rhamnus cathartica, Euonymus europæus*), there are but two planes of section, the median and the lateral, which will give exactly similar halves, though the flower is also symmetrically but diversely divisible in the diagonal planes (Fig. 323 *A*); or, again, where the flower is hexamerous (*e.g.* species of Sedum) it is symmetrically divisible in twelve planes, but the halves produced by the section in six of the planes are unlike those produced by section in the other six planes.

The symmetry may be *isobilateral*; in this case the flower is divisible into symmetrical halves in two planes, but the halves produced by section in one plane are unlike those produced by section in the other plane. Thus, a regular eucyclic dimerous flower (*e.g. Circæa lutetiana*, Fig. 323 *B*; *Fraxinus dipetala*), is symmetrically divisible in the median and lateral planes, but the halves produced by the median section differ from those produced by the lateral section. This is true also of some regular heterocyclic flowers, such as those of the Cruciferæ, Jasminum, *Olea europæa*, Cornus, Hamamelis, the whorls of which are 2- or 4- merous, and of the somewhat peculiar flower of Dicentra.

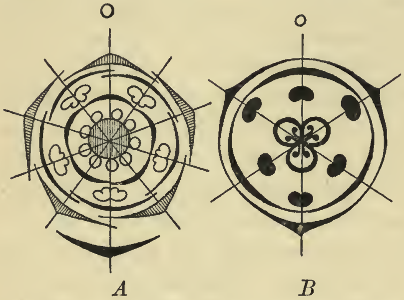

FIG. 322.—*A* Diagram of the pentamerous flower of Primula, showing the five planes of symmetry; the stamens are antipetalous; there are no prophylla. *B* Diagram of the trimerous flower of Lilium, showing the three planes of symmetry. (After Eichler.)

The symmetry may be *zygomorphic*, that is, the flower may be *monosymmetrical*, there being only one plane in which it is symmetrically divisible. This condition is to be found in regular heterocyclic flowers, and is the result of oligomery of the whorls, generally of the gynæceum, rarely of the andrœcium. Flowers of this type are common among Dicotyledons (*e.g.* in the Ribesiaceæ, Apocynaceæ, Boraginaceæ, Solanaceæ, Gentianaceæ, Campanulaceæ, Compositæ, Rosaceæ, Saxifragaceæ, Umbelliferæ, etc.), the oligomerous gynæceum having 1–4, generally 2, carpels, the rest of the flower being pentamerous or hexamerous. In this case the plane of symmetry is determined by the position of the carpels.

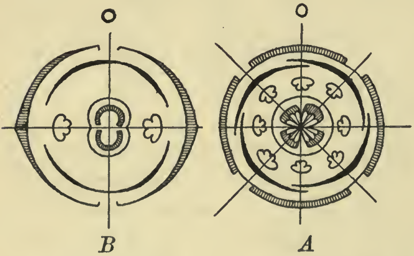

FIG. 323.—*A* Diagram of the tetramerous flower of Fuchsia, showing the four planes of symmetry. *B* Diagram of the dimerous flower of Circæa, showing isobilateral symmetry.

Thus, when there are two carpels, the plane of symmetry is generally median because the carpels are frequently median or, less commonly, lateral (*e.g. Vinca minor*, *Ribes alpinum*, Fig. 324 *A*, *B*): but when the two carpels are placed obliquely (*e.g.* many Solanaceæ, such as Petunia, Fig. 324 *D*; Datura, Hyoscyamus: Menyanthes among Gentianaceæ, Fig. 324 *F*; Saxifraga), the plane of symmetry is oblique. Similarly, when the gynæceum is monomerous or trimerous, if it is so situated that its plane of symmetry coincides with the median plane of the flower (*e.g.* with monomerous gynæceum, Mirabilis, Mahonia; with trimerous gynæceum, Polemonium; some Caryophyllaceæ including most species of Silene, Stellaria, Spergularia, etc.; some Campanulaceæ; *Deutzia crenata; Sambucus Ebulus*, etc.), then the plane of symmetry of the flower is the median plane; but when the plane of symmetry of the gynæceum is oblique (*e.g.* with monomerous gynæceum, Berberis, Anacardium; with trimerous gynæceum, some Malpighiaceæ, Æsculus) the plane of symmetry of the whole flower is oblique likewise.

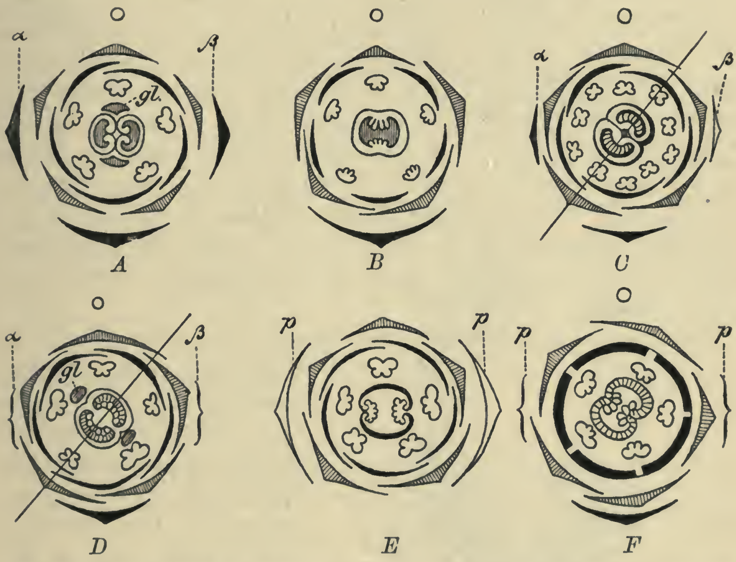

Fig. 324.—Floral diagrams illustrating monosymmetry due to oligomery of the gynæceum : *A Vinca minor*; *B Ribes alpina*; in these the plane of symmetry is median : *C* Saxifraga; *D* Petunia; in these the plane of symmetry is oblique: *gl* gland: α β prophylla: *E* terminal flower of *Gentiana verna*, with median plane of symmetry: *F* lateral flower of *Menyanthes trifoliata*, with oblique plane of symmetry; *p p* prophylla. (After Eichler.)

Monosymmetry in consequence of an oligomerous andrœcium is less common; a good instance is afforded by *Commelyna cœlestis*, in which flower the plane of symmetry is oblique (Fig. 325). Monosymmetry is also characteristic of *irregular* flowers, whether eucyclic or heterocyclic; of flowers, that is, in which the members of one or more whorls differ in various respects among themselves, accompanied frequently by a reduction in the typical number of members in one or other of the whorls, frequently of the andrœcium: it is, in fact, to irregular flowers that the term *zygomorphic* is specially applied in Descriptive Botany. Such a flower usually presents a clear distinction into two diverse portions, an anterior and a posterior, separated by the lateral plane, whilst the two lateral halves about the median plane are symmetrical; hence it is clearly *dorsiventral* (Fig. 326).

FIG. 325.—Floral diagram of *Commelyna cœlestis* showing monosymmetry due to oligomery of the andrœcium: the plane of symmetry is oblique: the three black stamens are sterile, and the postero-lateral staminode is often absent: the antero-lateral fertile stamen has a broader connective than the others. (After Eichler.)

Dorsiventrality is presented by some flowers which, so far as their early development is concerned, or even so far as is shown by their floral diagram, are actinomorphic, isobilateral, or simply zygomorphic, the dorsiventrality being due to the subsequent irregular development of some of the floral leaves; as in some eucyclic flowers (*e.g.* among Monocotyledons, Agapanthus, Alstroemeria, Amaryllis, Gladiolus; among Dicotyledons, Dictamnus, and other Ruteæ, species of Impatiens, Pelargonium), and in some heterocyclic flowers (*e.g.* some Scrophulariaceæ, Labiatæ, some Caprifoliaceæ,

FIG. 326.—Dorsiventral flower of a Heracleum (mag.

Violaceæ, Echium, Lobelia, Orchidaceæ, the marginal flowers of the inflorescences in some Umbelliferæ and the ray-florets of some Compositæ). The degree of irregularity in these flowers varies widely; the irregularity may be very slight, due to the more active growth of the leaves (perianth-leaves only, or stamens also) of one half of the flower, either the posterior (*e.g.* Gladiolus), or the anterior (*e.g.* Amaryllis), which causes an upward or a downward curvature; this is more marked in Dictamnus where the calyx and corolla tend to form two lips, an upper and a lower; this *bilabiate* form of flower is more fully developed in the calyx and corolla of the Labiatæ, the corolla (*personate*, the lips being closed) of the Scrophulariaceæ, and of the Orchidaceæ and Lobelia. In not a few cases the irregularity of the flower is increased by the development of spurs from some portion of the perianth (*e.g.* among Monocotyledons, Orchis, Rhinopetalum, from the corolla; among Dicotyledons, Linaria, Viola, from the corolla; Pelargonium, from the calyx). A remarkable morphological feature is offered by the flowers of Orchis and of Lobelia which are *resupinate*; that is, in consequence of torsion of the pedicel, the posterior side of the flower becomes anterior. The plane of symmetry is generally median in these flowers.

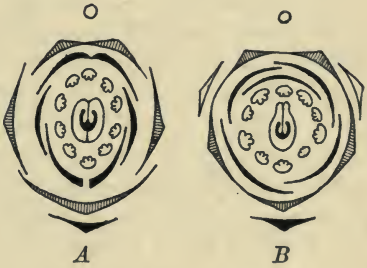

Fig. 327.—Diagram illustrating dorsiventral symmetry in leguminous flowers: *A Vicia Faba* (Papilioneæ): *B Cercis Siliquastrum* (Cæsalpinieæ): in both cases the odd sepal is anterior: the plane of symmetry is median.

In some few cases the irregularity, leading to dorsiventrality, is due, not to the unequal development of the floral leaves, but to the configuration of the floral receptacle, so that the floral leaves are not developed in a radially symmetrical manner (*e.g.* Reseda, Papilioneæ, Fig. 327).

When in irregular flowers the single plane of symmetry is the median plane, the flower is dorsiventral: but there are other cases (*e.g.* flowers of some Fumariaceæ, Fumaria, Corydalis) in which the single plane of symmetry is the lateral; these flowers are therefore not dorsiventral, that is, they have not antero-posterior, but lateral, asymmetry. The zygomorphic symmetry of a flower is indicated in its floral formula by symbols; when the plane of symmetry coincides with the median plane the symbol $\downarrow$ is used, and when it coincides with the lateral plane the symbol $\rightarrow$.

Sometimes regular flowers are developed by plants which usually produce irregular flowers: these exceptional flowers are termed *peloria*. This is due in some cases to the fact that the primitive number and arrangement of the floral organs is not disturbed by the irregular development of the parts which usually takes place: such cases are distinguished as *regular peloria* (*e.g.* Viola, Gloxinia, Labiatæ, etc.) In other cases the peloric flower is to some extent the result of the symmetrical development of the irregularity (*e.g.* the development of five spurred petals and five stamens in Linaria). Dorsiventral flowers are, generally speaking, such as are borne laterally on the inflorescence; whilst the terminal flowers (which may be regarded as peloric) are frequently regular. Peloric lateral flowers are, however, known to occur.

There remain to be considered those flowers which cannot be symmetrically divided in any plane: such flowers are *asymmetric*. Amongst these are to be included most of the acyclic or hemicyclic flowers in which the number of members is high and the divergence variable (*e.g.* Calycanthus, some Ranunculaceæ, etc.): the asymmetry of most of these is approximately, though not quite accurately, actinomorphic, but in some it is dorsiventral (*e.g.* Delphinium, Aconitum). Asymmetry is rare in cyclic flowers, but is to be found in some heterocyclic flowers: for instance, in Tropæolum, Canna and other Marantaceæ, Valeriana and other Valerianaceæ, where the asymmetry is dorsiventral and is due to oligomery and irregularity combined, whilst in other cases (*e.g.* some Paronychieæ, Fig. 328 *C*) it is due merely to oligomery.

The Floral Organs.

The *Perianth* is completely absent, that is, the flower is *achlamydeous*, in a few families (*e.g.* Piperaceæ, Araceæ, Graminaceæ, many Cyperaceæ, Salicaceæ). When present, it is usually differentiated into calyx and corolla, the flower being termed *dichlamydeous* or *biseriate*: when the calyx and corolla clearly differ from each other in colour, texture, etc., the flower is said to be *heterochlamydeous*; for instance, when the calyx is green and the corolla highly coloured (as in most Dicotyledons, and in some Monocotyledons such as Tradescantia and Commelyna); or when the calyx is coloured (petaloid) and the petals reduced to nectaries (as in Helleborus and other Ranunculaceæ). When the perianth-leaves are all alike, the flower is said to be *homochlamydeous*. This condition may be due to different causes in different cases: the flower is sometimes homochlamydeous, even though calyx and corolla are differentiated, because the sepals and petals are very similar, as in most Monocotyledons where the sepals are often petaloid: in other cases the flower is homochlamydeous, because only one series of perianth-leaves is developed; that is, because the flower is *monochlamydeous.* The flower may be monochlamydeous because, though typically dichlamydeous, either the calyx or the corolla is suppressed (*e.g.* calyx suppressed in some Umbelliferæ and Compositæ; corolla suppressed in most Thymelæaceæ, Paronychieæ, Glaux, some Rosaceæ, such as Alchemilla and Sanguisorba); where the corolla is suppressed or rudimentary the calyx is frequently petaloid (*e.g.* Clematis, Anemone, Caltha, and other Ranunculaceæ): or the flower may be monochlamydeous merely because the perianth is undifferentiated (simple), and is then generally sepaloid (*e.g.* Urticaceæ, Betulaceæ, Proteaceæ, Chenopodiaceæ, etc.), or petaloid (*e.g.* some Amarantaceæ, Phytolaccaceæ, Nyctaginaceæ).

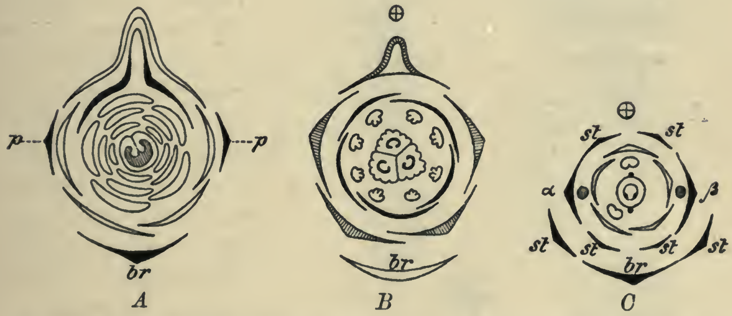

Fig. 328.—Floral diagrams illustrating asymmetry. *A* **Dorsiventrally asymmetrical hemicyclic flower of** ***Delphinium Ajacis*** **:** *B* **Dorsiventrally asymmetrical heterocyclic flower of** ***Tropæolum majus*** **:** *C* **Asymmetry due to oligomery in** ***Anychia dichotoma*** **(Paronychieæ):** *br* **subtending bract;** *p-p*, *α β* **prophylla;** *st* **stipules of bract and prophylla. (After Eichler.)**

It is not always easy to determine whether a homochlamydeous flower is dichlamydeous or monochlamydeous; but the decision is facilitated by the consideration that, as a rule, the calyx and corolla each consist of a single whorl of perianth-leaves in the Monocotyledons, whereas in Dicotyledons the calyx generally consists of two whorls. Hence, in the absence of contrary information afforded by its development, a homochlamydeous flower having two perianth-whorls should, if a Monocotyledon, be regarded as being probably dichlamydeous; whereas, if a Dicotyledon, it should be regarded as probably monochlamydeous, the two whorls representing either a calyx or a simple perianth.

The individual leaves of the perianth may be either perfectly separate (*eleutheropetalous* or *polypetalous* corolla, *eleutherosepalous* or *polysepalous* calyx), *e.g.* Ranunculus; or they may cohere from the base upwards, so as to form a longer or shorter tube, which divides at its upper end into as many teeth or lobes as there were originally leaves (*gamosepalous* calyx, *gamopetalous* corolla) (Fig. 329 *A B C c* and *B k*); *e.g.* the Primrose and the Tobacco plant. In Dianthus (the Pink) the sepals alone are coherent, as also in Daphne (Fig. 329 *D*) where the corolla is absent. More rarely all the leaves of the perianth cohere to form one tube, *e.g.* the Hyacinth and allied genera; the six lobes of the tube correspond to the three sepals and the three petals. The simple perianth also may consist of separate leaves (*eleutherophyllous* or *polyphyllous* perianth), *e.g.* Amarantus, or the leaves may be coherent (*gamophyllous*), *e.g.* Aristolochia.

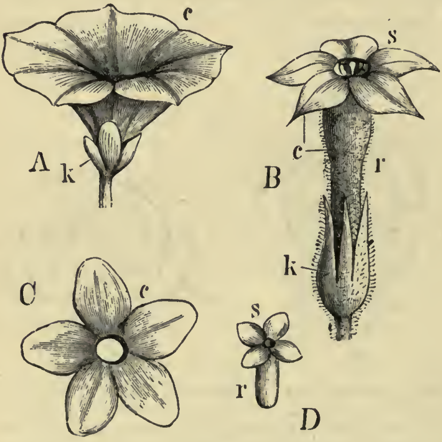

FIG. 329.—Cohesion of sepals and petals. *A* Flower of *Convolvulus arvensis*, with a funnel-shaped corolla (c); and a 5-partite calyx (*k*). *B Nicotiana Tabacum*, with a 5-cleft calyx (*k*); tubular corolla (*r*), with a distinct 5-toothed limb (*s*). *C* The rotate corolla of Sambucus. *D* Gamosepalous calyx of *Daphne Mezereum*; *r* the tube; *s* the limb.

The degree of division presented by gamophyllous perianths into teeth or lobes is indicated by the same terms which are used in describing the incision of the leaf-blade (page 54). The form of the gamopetalous corolla may be *campanulate*, as in the Campanula; *funnel-shaped* (or *infundibuliform*), as in the Bindweed (Fig. 329 *A*); *rotate*, as in the Elder (Fig. 329 *C*). The upper and lower portions may frequently be distinguished, the lower as *the tube* (Fig. 329 *B r*), the upper expanded part as *the limb* (Fig. 329 *B s*). Other peculiarities of form are connected with the symmetry of the flower (page 511).

The petal frequently consists of two parts, the *claw* and the *limb*, as in the Pink (Fig. 330 *A B*). The *Corona* (paracorolla) in the Narcissus and Lychnis is formed by ligular outgrowths from the claws (Fig. 330 *B l*). Any segmentation of the petal, as in the Pink (Fig. 330 *A*) is unusual; emarginate or obcordate petals are more common. In many cases the petals have spur-shaped appendages (Violet, p. 511), or they are prolonged at the base into tubes, as in Helleborus and Aconitum. This peculiarity is connected with the secretion of the nectar (page 526).

The Reproductive Organs of the Flower are sporangia of two kinds, microsporangia and macrosporangia, borne usually on sporophylls, though sometimes directly on the floral axis. The flower is usually ambisporangiate (☿, hermaphrodite, see p. 432); but it is not infrequently monosporangiate (unisexual), in which case the flowers are either microsporangiate (♂, staminal) or macrosporangiate (♀, carpellary). The plants which have monosporangiate flowers may be either monœcious (*e.g.* Zostera, Arum, Carex, Typhaceæ, Zea, Betulaceæ, Euphorbia, Buxus, Juglans, Quercus, etc.): or diœcious (*e.g.* Pandanaceæ, some Palms, Naias, Vallisneria, Hippophae, Cannabinaceæ, Salicaceæ, Mercurialis, Viscum, Empetrum, Feuillea, etc.): or *polygamous.* Of polygamy there are several varieties: thus, the plant may bear ambisporangiate flowers and staminate flowers (*e.g.* Veratrum, Ptelea, *Æsculus Hippocastanum*, Celtis); or ambisporangiate flowers and carpellary flowers (*e.g. Thymus vulgaris* and *T. Serpyllum*, *Parietaria diffusa* and *P. officinalis*): or it bears ambisporangiate flowers and both staminate and carpellary flowers (*e.g. Fraxinus excelsior*, *Saponaria ocymoides*).

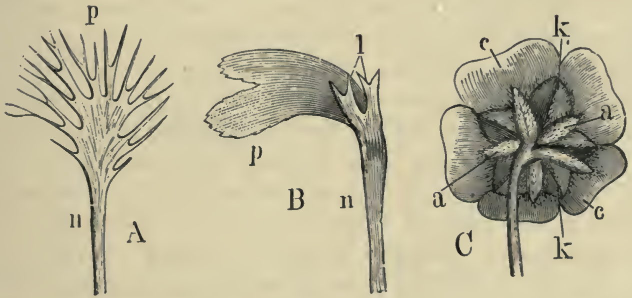

Fig. 330.—*A* Petal of *Dianthus superbus*, with (*n*) the claw and (*p*) the limb, much divided. *B* Petal of Lychnis: *n* claw; *p* limb; *l* ligula. *C* Flower of Potentilla, seen from below: *c* corolla; *k* calyx; *a* epicalyx.

Some flowers are probably primarily monosporangiate (p. 505); that is, there is no reason to believe that the monosporangiate condition is due to the suppression of either micro- or macrosporangia (*e.g.* Hemp, Oak, Walnut, Poplar, Willow). Others are secondarily monosporangiate; that is, there is reason to believe, either from their development and structure, or from their relation to allied ambisporangiate forms, that they are typically ambisporangiate, but have become monosporangiate by suppression: thus, in the Cucurbitaceæ some genera (*e.g.* Cucurbita, Cucumis, Bryonia, etc.) have monosporangiate flowers, whilst in others (*e.g.* Schizopepon) the flowers are always ambisporangiate; similarly, in the Caryophyllaceæ, the flowers are generally ambisporangiate, but in the species *Lychnis vespertina* and *L. diurna* they are monosporangiate; and again in the Polygonaceæ certain species of Rumex (*R. Acetosa*, *Acetosella*, etc.) alone are monosporangiate: in some monosporangiate flowers traces of the missing organs are to be found, such as staminodia in carpellary flowers (*e.g.* Cocculus and other Menispermaceæ, Feuillea among the Cucurbitaceæ; *Laurus nobilis*), or rudimentary pistils in staminate flowers (*e.g.* *Rhamnus cathartica*, Cocculus, *Lychnis vespertina* and *diurna*).

It sometimes happens that typically diœcious plants become exceptionally monœcious (*e.g.* development of ♀ flowers on ♂ plants of *Myrica Gale* and *Cannabis sativa*; or of ♂ flowers on ♀ plants of *Cannabis sativa* and *Mercurialis annua*): or that a typically diclinous monœcious plant bears some monoclinous flowers (*e.g.* Ricinus).

The *Andrœcium* comprises the microsporophylls (one or more) of the flower, the stamens. Each stamen usually consists of two parts; a slender stalk called the *filament* (Fig. 331 *s*), and a placental portion which bears the pollen-sacs (Fig. 331 *Dp*), known as the *anther* (Fig. 331 *a*). The anther consists of two longitudinal halves, termed *thecæ*, each of which usually contains two pollen-sacs; these two halves are united by the placental portion of the filament which is known as the *connective* (Fig. 331 *c*). This is occasionally very narrow, so that the two halves of the anther lie close together (Fig. 331 A_1 *a*): in this case it may be that the anther is not sharply marked off from the filament, and is attached throughout its whole length to the filament (*adnate*, Fig. 332 *C*): when the anther is sharply marked off from the filament, it may be attached to the filament by its base, when it is said to be *innate* or *basifixed* (*e.g.* Tulip); or the filament is inserted in the middle of its dorsal surface, when it is *dorsifixed* (Fig. 331 *A*); in the last case it may be articulated as by a joint, so that the anther with the connective can oscillate on the apex of the filament (*versatile anther*, Fig. 331 *C*), as in Grasses and some other plants. But the connective is often broader, so that the two halves of the anther are widely separated (Fig. 331 *B*); it may be much elongated (*distractile*) and very delicate, so that, with the filament, it forms a T-shaped body (Fig. 331 *C*); in this plant, the Sage, the further peculiarity is exhibited that one-half of the anther is abortive and is modified for another purpose. It is only

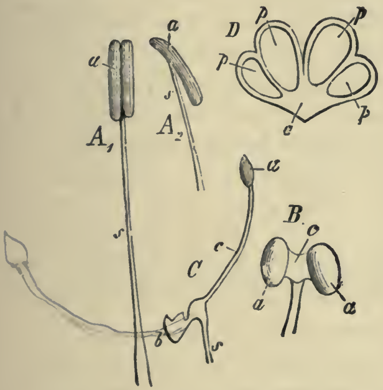

Fig. 331.—Stamen: A_1 Of Lilium: *s* filament; *a* the dorsifixed anther. A_2 Side view. *B* Of Tilia: *c* connective. *C* Of Salvia, with dorsifixed versatile anther: *b* is the half of the anther that has been modified. *D* Transverse section of the anther of Hypericum (mag.): *p* the 4 pollen-sacs; *c* connective.

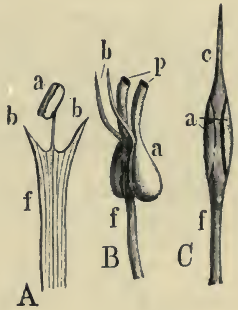

Fig. 332.—*A* Stamen of Allium. *B* Of *Vaccinium Myrtillus*. *C* Of *Paris quadrifolia* (mag.): *f* filament; *c* connective; *a* anther; *b* appendages; *p* the pores by which the anther opens.

rarely, as in Herb Paris, that the connective is prolonged beyond the anther into a point, or into a bristle as in the Oleander.

The filament is usually round and stalk-like, of a delicate coloured or colourless tissue, with a central vascular bundle; it is occasionally flattened; when it is very short or absent the anthers are *sessile*.

In some plants, *e.g.* Allium (Fig. 332 *A*), the filament has what appear to be stipular appendages; in others, *e.g.* Erica (Fig. 332 *B*) and Asclepiadaceæ, the anther is furnished with appendages, such as spurs and so forth: in Viola, the spurs borne by the two anterior stamens are glandular. In certain plants the stamens, that is to say the filaments, branch; either, like most leaves in a plane perpendicular to the median plane, as in Myrtaceæ and Fumariaceæ, or in various planes, as in Ricinus (Fig. 333) and Hypericaceæ; an anther is borne on each of the branches of the filament.

Somewhat similar in appearance, but essentially different in structure, are the coherent stamens of the Papilioneæ and other plants. The stamens of each flower may be coherent into one or more bundles. The arrangement becomes complicated when the filaments are at the same time coherent and branched as in the Malvaceæ. When the filaments are all coherent into a single bundle (*e.g.* Malvaceæ), they are said to be *monadelphous*: when in two bundles (*e.g.* some Papilioneæ, Fumariaceæ), they are *diadelphous*; when in several bundles (*e.g.* Hypericaceæ), they are *polyadelphous*. In the Compositæ (*e.g.* Sunflower and Thistle), though the filaments are free, the anthers become coherent or *syngenesious*. When the stamens are quite free from each other they are said to be *polyandrous*.

A variety of the monadelphous condition is found in the ♂ flowers of certain Araceæ, where the stamens are united into a central column termed a *synandrium*.

Besides these varieties of *cohesion*, *adhesion* frequently occurs; that is the filaments adhere to other portions of the flower, particularly of the perianth, so that they—or when they are very short, the anthers—appear to be inserted not upon the axis of the flower, but upon the leaves of the perianth (*epipetalous* or *epiphyllous*). This condition is most frequently present when the petals themselves are connate and form a tubular corolla, *e.g.* Primula. The adhesion of the stamens to the carpels is of rarer occurrence (*e.g.* Orchidaceæ, Stylidium, and Aristolochia); the flower is then termed *gynandrous*.

In many flowers it happens that certain filaments, occupying a definite position with regard to the other parts of the flower, are longer than the others; thus, of the six stamens of the Cruciferæ (*e.g.* Wallflower and Cabbage), four are much longer than the other two; of the four stamens of the Labiatæ (*e.g.* Lamium), two are longer than the other two. In the former case the stamens are said to be *tetradynamous*, in the latter *didynamous*.

Stamens which bear no anthers are termed *staminodia*: they are to be found in flowers which have become monosporangiate by suppression (*e.g.* carpellary flowers of *Laurus nobilis*), as well as in others where suppression of the pollen-sacs is incomplete (*e.g.* Canna, Trollius, some Lauraceæ); in the latter case the staminodia are frequently petaloid. In many acyclic flowers (*e.g.* Nymphæa), the stamens and the petals are connected by intermediate structures, of which it is difficult to say whether they are to be regarded as petaloid stamens or as staminoid petals.

The *Microsporangia* or *Pollen-Sacs* are borne on the anther. There are commonly four of them (*quadrilocular* anther), two forming a sorus in each longitudinal half (or theca) of the anther, situated usually side by side, but sometimes (Lauraceæ) one above the other; in the former case the typical arrangement seems to be that of each pair of pollen-sacs one belongs to the anterior or inner surface of the anther, the other to the posterior or outer surface.

In some cases, however, there are but two pollen-sacs — (*bilocular* anther): this may be due to the non-development of one longitudinal half of the anther (*e.g.* Cucurbitaceæ, Salvia, Canna); or to branching (*e.g.* Adoxa, Malvaceæ); or to the abortion of one pollen-sac, generally the posterior one, of each pair (*e.g.* Asclepiadaceæ, Grubbia); or (some Lauraceæ) of the upper or lower one of each pair; or, finally, to the early fusion of the archesporia of two adjacent pollen-sacs (some Orchidaceæ). In the Araceæ the process of fusion is carried to such an extent that all four archesporia fuse, so that the anther is unilocular.

Fig. 333.—Part of a staminal flower of *Ricinus communis* cut through lengthways: *f f* the basal portions of the compoundly-branched stamens; *a* the anthers. (After Sachs.)

Rarely (*e.g.* Sarcophyte, among Balanophoraceæ) the anther bears numerous pollen-sacs: the pollen-sac is sometimes multilocular (see p. 433).

Each pollen-sac encloses an archesporium from which the mother-cells of the microspores (pollen-grains) are developed by division: each group of spore-mother-cells is invested by a layer of granular cells, the *tapetum* (Fig. 281 *t*), which eventually becomes disorganised: externally to this is the wall of the pollen-sac consisting of one or more layers of cells with usually reticulately thickened walls, followed by the epidermis at the surface.

The pollen-sacs dehisce usually by a longitudinal slit which, when the anther is quadrilocular, is generally so situated that it at once opens into both the pollen-sacs of each half of the anther, and frequently the tissue separating each pair of pollen-sacs becomes dried up and ruptured whilst the anther is ripening: sometimes the dehiscence of the pollen-sac is transverse (Alchemilla); sometimes it is valvular (Lauraceæ, Berberidaceæ); or by apical pores (Ericaceæ, Polygalaceæ). Though in a quadrilocular anther the pollen-sacs typically belong, two to the inner (ventral), two to the outer (dorsal), surface of the anther, it frequently happens that in the course of their development they become somewhat displaced, so as to appear all to belong to either the inner or the outer surface; hence, when dehiscence takes place, the pollen is shed, in the former case, towards the centre of the flower, when the anthers are said to be *introrse*; and, in the latter case, towards the periphery of the flower, when the anthers are said to be *extrorse.* These terms are similarly applicable in the case of bilocular anthers. Introrse anthers are the more common; extrorse anthers occur in the Calycanthaceæ, Aristolochiaceæ, Iridaceæ, Juncagineæ, Araceæ, and in various genera of other orders. In rare cases some of the anthers of the flower are introrse, and others extrorse, as in some species of Polygonum (*P. Bistorta, tataricum, aviculare*, etc.), when the anthers of the outer whorl are introrse, and those of the inner whorl extrorse; and as in most Lauraceæ, where the anthers of the innermost staminal whorl are extrorse, whilst those of the outer whorls are introrse.

The *Microspores* or *Pollen-grains.* The essential features in the structure and development of the microspores have been already fully described (see pp. 125 and 434).

The shapes of the pollen-grain are very various (p. 436): it may be spherical, oval, triangular, etc., or long and cylindrical (confervoid) as in the Naiadaceæ. In Halophila the shortly cylindrical pollen-grains adhere so as to form filaments.

On germination the pollen-grain gives rise to one or more pollen-tubes, which consist of outgrowths of the intine: these penetrate the exine (when present), either rupturing it irregularly, or at determinate points where the exine is thinner and less resistent (*e.g.* Onagraceæ, Malvaceæ), or where there are lid-like areas which are easily removed (*e.g.* Cucurbitaceæ, Fig. 282). These points are definite in number (1, 2, 3, 4, or more), sometimes very numerous (Malvaceæ).

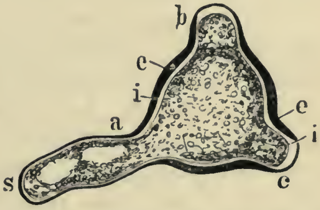

FIG. 334.—Germinating pollen-grain of Epilobium (highly mag.) bearing a pollen-tube *s*; *e* exine; *i* intine; *a b c* the three spots where the exine is thicker in anticipation of the formation of the pollen-tube developed in this case at *a*.

The *Gynæceum* or *Pistil* is always the terminal structure of the flower, occupying the apex of the floral axis. It consists of the *macrosporophylls* or *carpels*, which, in the Angiosperms form the whole or part of the *ovaries*, that is, closed cavities containing the ovules. If in a flower where there are several carpels, each of them closes by the cohesion of its margins, they form so many ovaries; the gynæceum is then said to be *apocarpous* (Fig. 335 *A*), *e.g.* Ranunculus, Pæonia, and Butomus; if there is only one carpel (Fig. 335 *B*), the pistil is said to be apocarpous and *simple*; if several carpels in one flower cohere and form a single ovary (Fig. 335 *C*), the gynæceum is said to be *syncarpous*, *e.g.* Poppy and Lily. Intermediate forms occur in that the carpels may cohere by their lower ends whilst their upper ends remain free (Fig. 335 *D*).

The ovary is said to be *monomerous* when it is formed of only one carpel (Fig. 336 *A*), the margins of which cohere on the side opposite to the midrib. The outer side along which the midrib runs is the dorsal surface (Fig. 336 *A r*), and the midrib itself is the *dorsal suture*; opposite to it is the line of cohesion, the *ventral*

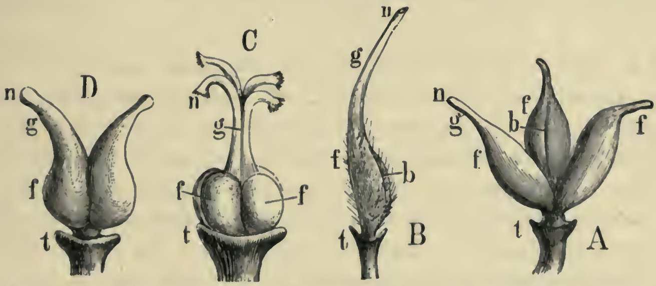

FIG. 335.—*A* Apocarpous gynæceum of Aconite. *B* Simple apocarpous gynæceum of Melilotus. *C* Tetramerous syncarpous gynæceum of *Rhamnus cathartica*. *D* Ovary of Saxifraga, formed of two carpels which diverge towards the top: *t* torus; *f* ovaries; *g* style; *n* stigma; *b* ventral suture.

suture, which runs therefore along the ventral surface. The cavity thus enclosed (*loculus*) is not usually divided by dissepiments, but it is a simple cavity, as in the Vetch; such an ovary is said to be *unilocular*. False or spurious dissepiments, formed by growths on the inner surface, occur in some few instances, as in Astragalus.

When, on the other hand, several carpels cohere to form a syncarpous ovary, it is *polymerous* (*di- tri- or tetra-merous*, etc). The syncarpous ovary is unilocular (Fig. 336 *B*) when the individual carpels cohere simply by their edges without any portion of them projecting inwards; but if the margins project into the cavity so as to form incomplete longitudinal dissepiments, the ovary is *chambered* (Fig. 336 *C*), *e.g.* Poppy; but since the chambers are open towards the centre, the ovary is still unilocular. When the margins form dissepiments which meet in the middle, the ovary is *multilocular*; sometimes the margins turn outwards again towards the circumference. In the last case the individual loculi are completely separated; but there are others in which the margins of the carpels do not extend so far towards the centre at the upper part as at the lower, but the two margins of each carpel simply cohere together above; consequently the lower part of the ovary is polymerous and multilocular, while the upper part is composed of a number of monomerous ovaries, *e.g.* Saxifraga (Fig. 335 *D*). In all these cases the floral axis may grow up into the interior of the cavity of the ovary, and when the ovary is multilocular the axis may coalesce with the dissepiments.

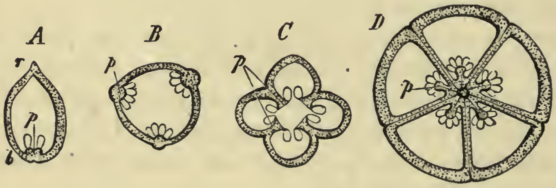

FIG. 336.—Transverse section of ovaries; *p* placenta. *A* Monomerous and unilocular; *r* dorsal suture; *b* ventral suture; *p* placentation marginal. *B* Polymerous and unilocular; placentation parietal. *C* Polymerous and many-chambered, but unilocular; placentation parietal. *D* Polymerous and multilocular; placentation axile.

False dissepiments may be formed in polymerous ovaries by ingrowths from the internal surface of the carpels; thus the ovary of the Boraginaceæ and Labiatæ is originally bilocular, but each loculus becomes divided into two by a false dissepiment, and when the fruit is ripe the four loculi separate completely; similarly, the unilocular ovary of the Cruciferæ becomes spuriously bilocular.

The inferior ovary of epigynous flowers (see p. 495) is rarely monomerous, that is to say, the cavity formed by the axis is but seldom closed by one carpel only: it is commonly polymerous, but it may be either unilocular or multilocular; in the latter case, the margins of the carpels grow down along the internal surface of the cavity.

In some bases the axis is prolonged between the carpels, constituting a *carpophore*, as in the Geraniaceæ and Umbelliferæ (Fig. 341).

The *Style* (Figs. 335 and 337) is the prolongation of the upper part of the carpel: it is commonly a slender cylinder, but sometimes it is leafy and petaloid (*e.g.* Iris). Monomerous ovaries have but one style; polymerous ovaries have as many styles as there are carpels, which may cohere throughout their whole length, or at their lower parts only, the upper parts remaining distinct; or they may remain quite free, and they may even branch. The style originally arises from the apex of the ovary, but it is frequently displaced forwards, by the vigorous development of the dorsal portion of the carpel, on to the inner side, so as to appear to be a prolongation of the floral axis (*gynobasic* style): this is conspicuous in the Boraginaceæ and Labiatæ, where it is surrounded by the four rounded loculi of the ovary which have been already mentioned (p. 522). The style is sometimes very short, and appears only as a constriction between the ovary and the stigma, as in the Poppy. In some rare cases it is hollow, but it is usually filled with a loose tissue, called *conducting tissue*, through which the pollen-tube can easily penetrate.

FIG. 337.—Gynæceum of the Lily: *f* ovary; *g* style; *n* stigma (nat. size).

The *Stigma* (Figs. 335 and 337 *n*) is usually terminal, but it may be lateral (*e.g.* Iris); it is distinguished by being covered with papillæ, or frequently with hairs, and by the secretion of a sugary fluid which retains the pollen-grains which fall upon it, and which promotes the development of the pollen-tubes. The stigma is often evidently distinct from the style, appearing as a lobed expansion; in other cases it seems to be merely a portion of the style at its end or sometimes on its side. In Papaver it is a sessile disk-shaped expansion on the upper surface of the ovary;

more rarely it is represented by bands of papillæ on the ovary itself, when it is said to be *pleurogynous.*

The number of the stigmata often affords a means of ascertaining whether the ovary is monomerous or polymerous: for instance, the ovary of the Compositæ seems, at first sight, to be monomerous; but the two short branches of the style, each bearing a stigma, show that it is dimerous. On the other hand, this character may be misleading: for instance, in various Grasses the ovary bears two or three stigmata, either directly, or springing from the style; hence it might be inferred that the ovary is di- or tri-merous, whilst as a matter of fact it is monomerous. In this respect some few other plants, belonging to the Naiadaceæ and other families, resemble the Grasses.

The *Macrosporangia* or *Ovules* are always enclosed in the cavity of the ovary, either singly or in larger or smaller number. Usually they may be readily seen to be developed on the carpels (Fig. 338 *A*, *B*, *C*), but in many cases they appear to be developed from the floral axis (Fig. 338 *D*, *F*, *G*). However, from careful comparative examination, it seems that the apparently axial ovules may be regarded in some cases as having been developed on the carpels, their position on the axis being merely the result of a more or less considerable subsequent displacement due to the coalescence of the carpels with the axis. That portion of the ovary which bears the ovules is called the *placenta.*

The ovules, when borne by the carpels, are but rarely developed over the whole surface of the carpel, but are confined to the margin: in other words the *placentation* is rarely *superficial* but generally *marginal.* Superficial placentation (Fig. 338 *C*) is to be found in Butomus, Nymphæa, and Nuphar, the dorsal suture (midrib) of the carpel being the only sterile portion of its internal surface. Of marginal placentation there are two varieties: in the one the ovary is syncarpous but unilocular, and the contiguous placental margins of the carpels constitute so many placentæ on the wall of the ovary, that is, the placentation is *parietal* (Fig. 336 *B*, *C*), as in the Violaceæ, Cruciferæ, Papaveraceæ, Ribesieæ, Orchidaceæ, etc.; in the other the ovary is syncarpous and multilocular, the margins of the carpels meeting in the centre and there bearing the ovules, so that each placenta is at the inner angle of each loculus, that is, the placentation is *axile* or *axillary* (Fig. 336 *D*, and Fig. 338 *B*): in a monomerous ovary (Fig. 336 *A*, and Fig. 338 *A*) the placentation is essentially parietal, but it is simply termed marginal.

The position of attachment is a point of descriptive importance, more especially where the number of ovules is small, or where there is but one, in the loculus. When the ovule is attached to the top of the carpel, so that it hangs into the loculus, it is said to be *pendulous*; when it is attached high up, but at the side, it is *suspended*; when it is attached to the side and projects straight, it is *horizontal*; when it is attached at the side, but towards the base of the carpel, and stands up into the loculus, it is *ascending*.

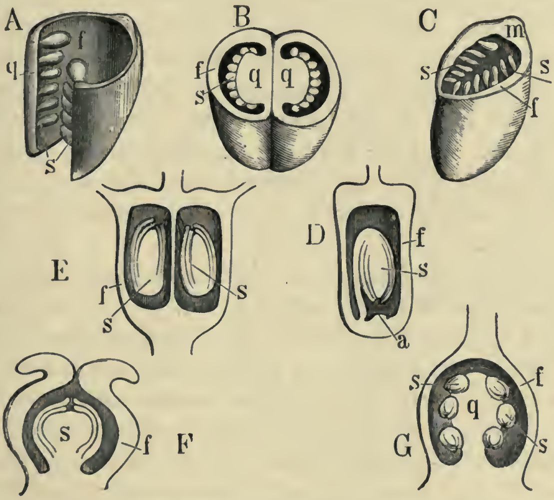

FIG. 338.—Diagrams of the different modes of Placentation. *A* Monomerous ovary of Helleborus, opened along the ventral suture; *s* the ovules on (*q*) the marginal placenta. *B* Transverse section of the ovary of Nicotiana: *f* wall of the ovary; *q* placenta, largely developed by the union of the margins of the carpels (axile placentation). *C* Transverse section of the ovary of Butomus. The ovules are scattered over the whole of the inner surface, except the midrib, *m* (superficial placentation). *D* Longitudinal section of an ovary of one of the Compositæ: *f* the wall; the erect, anatropous ovule (*s*) grows from the base by the side of the apex of the axis, *a*. *E* Longitudinal section of the ovary of one of the Umbelliferæ; in each chamber an anatropous ovule is suspended. *F* Longitudinal section of Rheum; a single erect orthotropous ovule grows at the apex of the floral axis. *G* Longitudinal section of the ovary of one of the Primulaceæ; the ovules grow on a prolongation of the axis (free central placentation). Fig. 336 *B* represents parietal placentation.

When the ovules are borne, either actually or apparently, by the axis, the placentation is said to be *axial*. When many ovules are borne on the axial placenta (as in the Primulaceæ, Santalaceæ, etc., Fig. 338 *G*), the placentation is termed *freecentral*. When there is but a single ovule in the loculus, the placentation is *basilar* or *basal*, and the ovule is *erect*: in this case the ovule is borne either terminally at the apex of the floral axis (*e.g.* Polygonum, Piper, Naias, Fig. 338 *F*); or laterally, below or behind the actual apex (*e.g.* Compositæ, Fig. 338 *D*).

For other descriptive terms relating to the ovule, refer back to p. 437.

The macrosporangium or ovule, consists primitively of a mass of cellular tissue, the *nucellus*, invested by one or two integuments, with a micropyle at the apex (see p. 436): generally speaking, two integuments are present in the Monocotyledons, in most polypetalous Dicotyledons (with exceptions such as some Umbelliferæ and Ranunculaceæ), and in the Cucurbitaceæ among Gamopetalæ; whereas there is only one integument in the Gamopetalæ (except Cucurbitaceæ) and in the polypetalous orders, Umbelliferæ and Ranunculaceæ. In some few cases (*e.g.* Santalaceæ, Loranthaceæ, Balanophoraceæ), where the development of the ovule is degraded in correlation with the parasitic habit of the plants, the ovule has no integument.

The *Macrospore* or *Embryo-sac.* The structure and development of the macrospore are described on p. 438.

Accessory Organs of the Flower. The most common of these is the *Nectary*, a glandular organ secreting odorous or sweet liquid, and thus attracting insects. The nectary is sometimes borne on some other organ—which is not thereby materially modified (*e.g.* petals of Ranunculus, stamen of Viola); or on a specially modified perianth-leaf (*e.g.* petals of some Ranunculaceæ, as Helleborus, Eranthis, Delphinium), or on staminodia (*e.g.* the posterior of the five stamens in Gesneraceæ; a whorl in Parnassia; one or more whorls in various Lauraceæ): in some cases it is borne on the carpels, in the septa of a multilocular ovary (septal glands of many Monocotyledons, Liliaceæ, Amaryllidaceæ, and Iridaceæ). Generally the nectary is borne on the floral axis, when it is described by the general term *disc*: it may be a single tubular outgrowth (Cristatella) or a flattened scale (other Capparidaceæ, some Resedaceæ); a single posterior scale; or several in a whorl, as scales or rounded prominences (*e.g.* Apocynaceæ; two in whorl in Vinca, Dipladenia; five in Forsteronia; many in Nerium: Cruciferæ, generally four: in Vitis five); or as a ring of tissue, round the base of the ovary (*e.g.* Rutaceæ, Anacardiaceæ, Rhamnaceæ, Celastraceæ); or on the upper surface of the inferior ovary (*e.g.* Umbelliferæ).

The position of the axial nectaries or discs is various: in some flowers it is *extra-staminal*, and then it is situated either between the andrœcium and the corolla (*e.g.* Capparidaceæ, Sapindaceæ, Resedaceæ), or, less commonly, between the corolla and the calyx (*e.g.* some Apocynaceæ, such as Nerium): in others it is *intrastaminal*, that is, between the andrœcium and the gynæceum (as in Rutaceæ, Rhamnaceæ, Celastraceæ, etc.). Again, the disc is generally hypogynous, but sometimes epigynous (Umbelliferæ).

Generally speaking, when the nectaries, of whatever kind, are towards the outside of the flower, the anthers are extrorse (*e g.* Ranunculaceæ); and when towards the centre of the flower, the anthers are introrse.

The most striking accessory structures are those of the Passion-flower: these are coloured filaments, borne in successive whorls (as many as five), between the corolla and the andrœcium: they are not glandular, neither can they be regarded as staminodia or as modified petals.

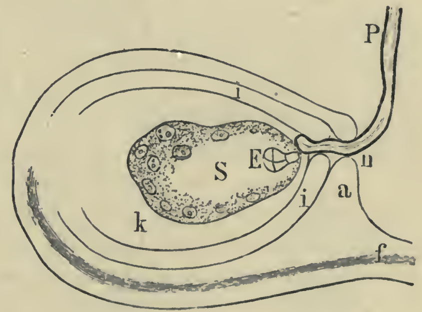

Fig. 339.—Diagram of an ovule shortly after fertilisation; *a* outer, and *i* inner integuments; *f* funicle: *k* nucellus. *S* Embryo-sac in which *E* is the embryo developed from the fertilised oosphere. The sac also contains the endosperm-cells which are being formed by free cell-formation. *P* The pollen-tube, passing through the micropyle, *n*.

The *General Histology* of the sporophyte is sufficiently treated of in Part II., and in the general account of the Phanerogams (p. 440).

The *Embryogeny* of the sporophyte is considered on p. 440.

The *Gametophyte* is considered on p. 447.

Fertilisation. After reaching the stigma the pollen-grains protrude the pollen-tubes which penetrate through the tissue of the style into the cavity of the ovary, and through the micropyle of each ovule to its nucellus (Fig. 339 *P n*). The time required by the pollen-tube for this process depends partly on the distance of the pollen-grain from the ovule and partly on the specific peculiarities of the plant; thus the pollen-tube of the Crocus takes only from one to three days to traverse the style, which is from five to ten centimetres in length; but in the Orchids, where the length of the style varies from two to three millimetres, several days, weeks, or even months are needed, and it is during this process that the ovules are formed in the ovary.

In Casuarina the pollen-tube does not enter the ovary by the style, but makes its way through the tissue of the wall of the ovary into the placenta, whence it penetrates into the ovule by the chalaza: the pollen-tube now grows towards the micropylar end of the ovule through one of the elongated sterile macrospores (see p. 438), and comes into close relation with the fertile macrospore, without, however, entering it; the male cell is apparently extruded from the pollen-tube into the macrospore, and enters the oosphere from below. The terminal portion of the pollen-tube becomes, in this case, completely abstricted off from the rest: and generally, when the pollen-tube is very long, the terminal portion becomes shut off from the rest by a plug of cellulose. Some other Amentales (Corylus, Carpinus, Alnus, Betula) also are *chalazogamic*.

The *Results of Fertilisation.* The *Seed* is described on p. 458.

The *Fruit.* In view of the variety in the structure and morphology of the fruit of Angiosperms, a somewhat detailed account of it is necessary.

The word *fruit*, in its strictest sense, means the whole product of the development of the gynæceum as a result of fertilisation. If other parts of the flower take part in the formation of the organ which is formed in consequence of fertilisation, and which contains the seed (of what, in short, is commonly called the fruit), it is termed a *spurious fruit* or *pseudocarp*. The apple, for instance, is such a spurious fruit, for the outer fleshy part belongs to that part of the axis of the perigynous flower which surrounds the ovaries and which still bears the sepals (Fig. 2 *A*). What are called the pips of the apple are the seeds. This kind of spurious fruit is termed a *pome*. The strawberry also is a spurious fruit: in it the receptacle, which belongs of course to the axis, developes largely and becomes fleshy and bears the true fruits (achenes) in the form of small hard grains. The fig is another example of a spurious fruit; it is in fact a fleshy receptacle (*i.e.* an axis) which bears a multitude of distinct flowers situated inside the cavity of the receptacle, and the individual fruits appear as hard grains; such a fruit is termed a *syconus*. Again, when the ovaries and floral envelopes of closely crowded flowers, as in the Mulberry and the Pine-apple, become succulent, a kind of spurious fruit is formed which is termed a *sorosis*.

In other cases, a husk, called the *cupule* is formed, which contributes to the formation of a spurious fruit: this is formed by the bracteoles and is not developed until after fertilisation; it may surround either a solitary distinct fruit, like the acorn-cup, or several distinct fruits, like the four-valved spiky husk of the Beech-tree or the prickly husk of the edible Chestnut.

When the fruit consists of one or more monomerous ovaries, it is said to be *apocarpous*: examples of this occur in Ranunculus, in the Raspberry, where the individual ovaries are succulent, and in the Star-Anise (Fig. 340). The individual fruits may be developed in very different ways; they may be dehiscent or indehiscent, dry or succulent.

When the fruit consists of a single polymerous ovary, it is said to be *syncarpous*. When the carpels of such a fruit separate septicidally during the process of ripening, so that it ultimately appears as if a number of distinct fruits were present, it is termed a *schizocarp*: it may thus split into only two distinct fruits, as in the Umbelliferæ (Fig. 341); or, as in the Geraniaceæ and many Malvaceæ, into several distinct fruits: each of them is termed a *coccus* or *mericarp*; the individual coccus is generally indehiscent (dehiscent in most Euphorbiaceæ).

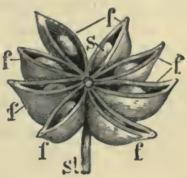

Fig. 340.—Fruit of *Illicium anisatum*: *st* peduncle; *f f* the separate fruits, each with a seed (*s*) forming an apocarpous fructification.

In various multilocular ovaries only one loculus becomes fully developed and bears seeds, as in Valerian, the Coco-Nut, and the Oak; the others are abortive. It sometimes happens in cultivated plants that the fruit becomes perfectly formed without any development of seed, as in a particular seedless variety of Grape, the Banana, the Pine-Apple, etc.

In all true fruits the wall of the ovary forms the *pericarp* or rind. In some more or less succulent fruits, the pericarp consists of three distinct layers; the external layer is the *epicarp*, the middle the *mesocarp*, and the innermost the *endocarp*.

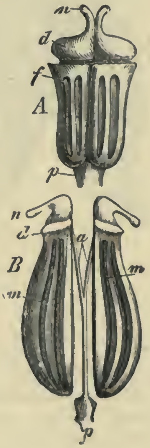

Fig. 341.—*Carum Carui*, one of the Umbelliferæ. *A* Ovary of the flower (*f*). *B* Ripe schizocarp which has divided into two cocci or mericarps (*m*), a portion of the median wall (*a*) forms the carpophore.

The following varieties of true fruits have been distinguished by the character of the pericarp, whether it is dry or succulent, hard or soft,—and by the dehiscence or indehiscence of the pericarp.

A. Dry Fruits. The pericarp is woody or coriaceous; when ripe, the sap has usually disappeared from all the cells.

I. *Dry Indehiscent Fruits.* The pericarp does not rupture, but encloses the seed until germination; the testa is usually thin, and frequently coalescent with the pericarp.

(1) One-seeded fruits:

(*a*) The *nut* (*glans*), *e.g.* Acorn, Hazel-Nut (but not the Walnut); the dry pericarp is hard and sclerenchymatous: it is inferior and syncarpous.

(*b*) The *achene* is superior and monomerous: the pericarp is thin and coriaceous; *e.g.* the Rose and the Buttercup. The similar fruit of the Compositæ is a *cypsela*; it is inferior and dimerous.

The fruit of Grasses, termed a *caryopsis*, is very similar to the achene; it differs from it in that the testa and the pericarp closely adhere, whereas in the achene they are not adherent.

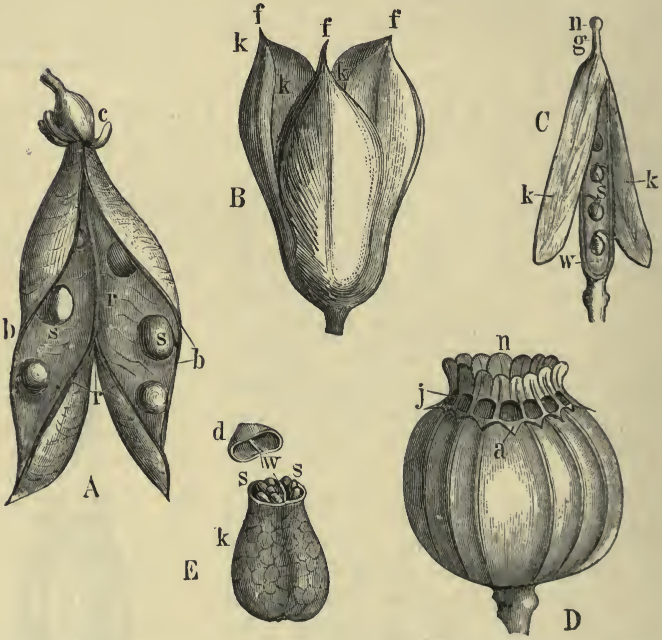

Fig. 342.—Dry dehiscent fruits. *A* The pod (legume) of the Pea: *r* the dorsal suture; *b* the ventral; *c* calyx; *s* seeds. *B* Septicidal capsule of *Colchicum autumnale*: *f f f* the three separating carpels. *C* Siliqua of Brassica; *k* the valves; *w* the dissepiment and placentæ (replum); *s* seeds; *g* style; *n* stigma. *D* Capsule, opening by pores, of *Papaver somniferum*, the Poppy; *n* stigma; *j* the pores which open by the removal of the valves (*a*). *E* Pyxidium of Hyoscyamus; *d* the lid; *w* the dissepiment; *s* seeds.

(2) Many-seeded fruits: these (*schizocarps*) commonly split into one-seeded fruits, which usually enclose the solitary seeds until germination: *e.g.* the Umbelliferæ (Fig. 341) and Maple, with two mericarps; the Geraniaceæ, with five mericarps; and most Malvaceæ, where the fruit is termed a *carcerule*, and splits into many mericarps (see p. 532).

The pericarp of dry indehiscent fruits is sometimes developed into a membranous wing (*e.g.* Ash, Elm, Birch); to such a fruit the term *samara* is applied: the fruit of the Maple is a double samara.

II. *Dry Dehiscent Fruits.* The pericarp ruptures and allows the seeds, which usually have a firm and thick testa, to escape:—they are commonly many-seeded.

(1) *Dehiscence longitudinal.*

(*a*) The *follicle*, consisting of a single carpel which dehisces along the ventral suture, where also the seeds are borne, *e.g.* Pæonia and Illicium (Fig. 340); but sometimes (*e.g.* Magnolia) along the dorsal suture: it is superior.

(*b*) The *legume* or *pod* likewise consists of but one carpel which dehisces along both the dorsal and ventral sutures (Fig. 342 *A*, transverse section Fig. 336 *A*): *e.g.* the Vetch, Pea, Bean, and many other Leguminosæ; in some cases (Astragalus) a spurious dissepiment occurs: it is superior.

The *lomentum* is a modification of the legume; it is constricted between the seeds, and it is either indehiscent or it breaks across, when ripe, at the constricted parts. It occurs in the Hedysareæ.

(*c*) The *siliqua* consists of two coherent carpels. The two carpels when ripe separate from the base upwards into two valves, leaving their margins (with the parietal placentæ and the spurious dissepiment) attached, as a frame or *replum*, to the apex of the pedicel; *e.g.* Rape, Mustard, and most of the Cruciferæ (Fig. 342 *C*): it is superior.

When the siliqua is short and broad, it is termed a *silicula*, as in Thlaspi and Capsella. In some cases, as in the Radish, the siliqua is jointed and indehiscent breaking transversely into one-seeded portions. It resembles the lomentum, and is therefore said to be *lomentaceous*.

(*d*) The *capsule* is derived from a polymerous syncarpous ovary which may be uni- or multilocular; it splits into two or more valves, either for a short distance only from the apex downwards, or down to the very base (Fig. 342 *B*). If the carpels become separated from each other, and in the case of multilocular ovaries this involves the splitting of the dissepiments (Fig. 343 *A*), the dehiscence is said to be *septicidal*; if, on the other hand, each carpel splits along its dorsal suture, the dehiscence is said to be *loculicidal* (Fig. 343 *B*). In either form of dehiscence in a multilocular ovary the placentæ may either adhere to the valves (Fig. 343 *B*), or remain united into a central column which is free from the valves; in the latter case the dehiscence is further described as being *septifragal* (Fig. 343 *C*).

The capsule is usually superior, but sometimes, as in Iridaceæ and Campanulaceæ, it is inferior; a special term, *diplotegium*, is applied to the inferior capsule by some authors.

(2) The form of capsule known as a *pyxidium* has a transverse dehiscence, *e.g.* in Plantago, Anagallis, Hyoscyamus (Fig. 342 *E*); the upper part falls off like a lid.

(3) The *porous capsule*, *e.g.* the Poppy (Fig. 342 *D*), sheds its seeds through small holes arising from the removal of small portions of the wall in certain spots.

B. Succulent Fruits. In these the pericarp is usually differentiated into layers, and some portion of it retains its sap until it is ripe, and usually becomes fleshy at that stage; it is indehiscent.

(1) The *drupe* (Fig. 344), is superior and monomerous, *e.g.* the Plum, Cherry; or syncarpous, *e.g.* the Walnut and Coco-Nut. The most internal layer, the endocarp, is very hard and sclerenchymatous (Fig. 344 *e*); it is commonly known as the *stone* in Plums, Peaches, etc., and encloses the seed until germination: the mesocarp is generally succulent, and the epicarp is a delicate membrane: when the fruit consists of several drupes, they are commonly termed *drupels* (*e.g.* Raspberry).

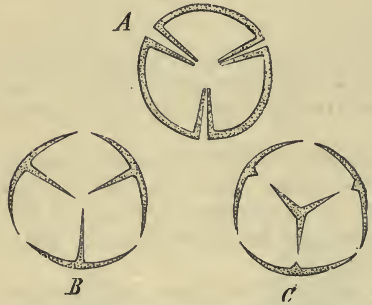

Fig. 343.—Diagrammatic sections of dehiscent multilocular capsules. *A* Septicidal, *B* loculicidal, dehiscence; *C* loculicidal septifragal dehiscence.

(2) The *berry* (*bacca*): the endocarp is soft and juicy as well as the mesocarp, so that the seeds are imbedded in the pericarp: there may be one seed only, as in the Date; or many, as in the Gourd, Currant and Grape: the fruit may have one loculus, as in the Grape and the Gourd, or several loculi, as in the Orange; and further. it may be superior, as in the Grape, Orange, and Lemon; or inferior, as in the Currant, the Gooseberry, and the Gourd.

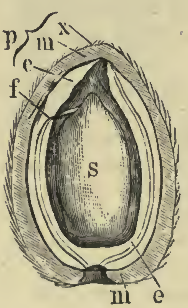

Fig. 344.—Longitudinal section of the drupe of the Almond: *s* the seed attached by the funicle (*f*); *e* the hard endocarp; *m* the mesocarp; and *x* the epicarp—these constitute the pericarp (*p*).

When the fruit is apocarpous and consists of many achenes, drupels, or follicles, it is termed an *etærio*; for instance, the fruit of the Buttercup, the Rose, and the Strawberry is an etærio of achenes; that of the Raspberry and the Blackberry is an etærio of drupels; that of the Tulip-Tree and of the Magnolia is an etærio of follicles.

The transition between a syncarpous and an apocarpous fruit can be readily traced in the Malvaceæ, from the loculicidal capsule of the Hibisceæ, through the schizocarpous carcerule of the Malveæ, to the fruit of the Malopeæ which resembles an etærio of achenes though the styles are coherent.

The Angiosperms are subdivided as follows:—

Class IX. Monocotyledones: the embryo has usually a single terminal cotyledon, and the growing-point of the primary stem is developed laterally: the ripe seed usually contains abundant endosperm: the vascular bundles of the stem are closed: the leaves commonly have parallel venation: the flower belongs usually to the pentacyclic trimerous type.

Class X. Dicotyledones: the embryo has usually two opposite cotyledons, and the growing-point of the primary stem is developed terminally: the ripe seed is commonly exalbuminous: the vascular bundles of the stem are usually open: the leaves commonly have reticulate venation: the structure of the flower varies, but it frequently belongs to the pentacyclic pentamerous type.

Class IX.—MONOCOTYLEDONES.

Although the seed typically contains endosperm, it contains none in certain orders; namely, the Orchidaceæ, most aquatic Monocotyledons (Alismales, Hydrocharidaceæ), and in some genera of Araceæ (Orontium, Symplocarpus, Scindapsus, Monstera, Amorphophallus). In the Scitamineæ perisperm is always present in the seed, either together with endosperm (Zingiberaceæ), or without endosperm (Musaceæ, Marantaceæ). In the albuminous seeds, the embryo is usually small in proportion to the endosperm (Fig. 345 I, *e*, *c*).

Whilst the single cotyledon of the embryo is, as a rule, terminal and the growing-point of the stem lateral, in some forms the growing-point of the stem is terminal (apical) on the longitudinal axis of the embryo (Dioscoreaceæ, Commelynaceæ, see p. 445). The growing-point of the primary stem frequently developes into a plumule. The axis of the embryo terminates posteriorly in a short radicle.

On germination, the upper end of the cotyledon commonly remains in the seed and absorbs the nutritious substances deposited in the endosperm (Fig. 345 *II.–IV.*); the lower part of the cotyledon elongates and pushes the rest of the embryo out of the seed. In Grasses the cotyledon has a peculiar shield-like form, and is termed the *scutellum* (Fig. 346 *sc*): in the ripe seed it almost entirely encloses the embryo, and is in contact by its outer surface

Gras

with the endosperm; during germination the cotyledon absorbs the nutritious matters contained in the endosperm, while the stem with the other leaves grows out of the seed. In other Monocotyledons either the cotyledon is a sheathing scale, or it is the first green leaf differing but little from the foliage-leaves which are subsequently developed.

blast

In many Grasses there is a scaly appendage borne opposite to the scutellum; this is termed the *epiblast*, and is sometimes regarded as a rudimentary second cotyledon (Fig. 346 *B*, *l*).

The primary root usually remains small and inconspicuous: in Grasses generally, the radicle begins to branch before it escapes through the micropyle on germination, so that the root is then fibrous; when this is the case the inadequate root-system is supplemented by the development of adventitious roots in succession at higher and higher levels upon the stem. The epiblema of the root is the external layer of the cortex (see p. 154)

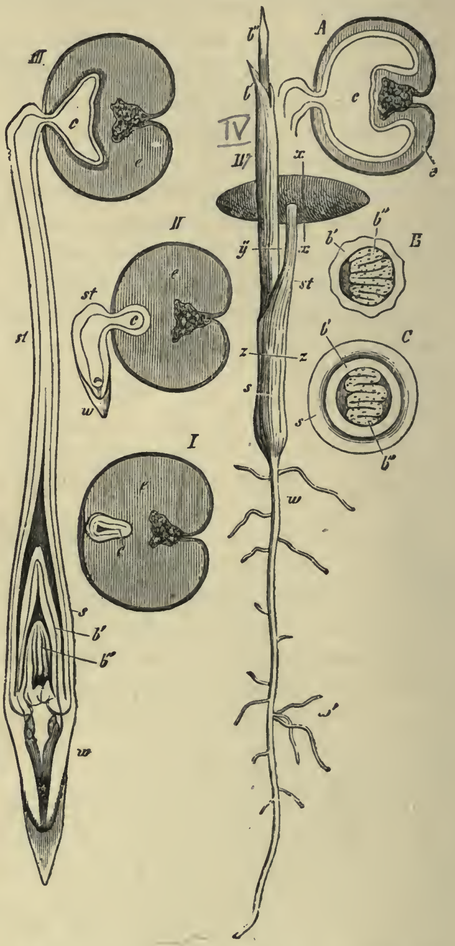

FIG. 345. — Germination of *Phœnix dactylifera*, the Date. *I.* Transverse section of the dormant seed. *III.*, *IV.* Different stages of germination (*IV.* the natural size). *A* Transverse section of the seed at *x x* in *IV.* *B* Transverse section of the seedling at *x y*: *C* at *z z*. *e* The horny endosperm; *s* the sheath of the cotyledon; *st* its stalk; *c* its apex developed into an organ of absorption which gradually consumes the endosperm and at length occupies its place; *w* the primary root; *w′* secondary roots; *b′ b″* the leaves which succeed the cotyledon; (*b″*) becomes the first foliage-leaf, in *B* and *C* its folded lamina is seen cut across. (After Sachs.)

The stem of Monocotyledons is traversed longitudinally (Fig. 132, p. 172) by scattered closed vascular bundles (Fig. 137); it has therefore no growth in thickness by the means of cambium. In a few genera only, as Yucca and Dracæna, it grows subsequently in thickness by the formation of meristem in the pericycle from which additional closed vascular bundles are developed (see p. 205, and Fig. 154).

The axis of the embryo in many cases continues to be the main axis of the plant; at first it is thin and weak, and since no secondary growth in thickness of the stem takes place, and since the successive portions of the stem are thicker and more vigorous, the whole stem gradually assumes the appearance of an inverted cone; but when the plant has reached a certain height it may

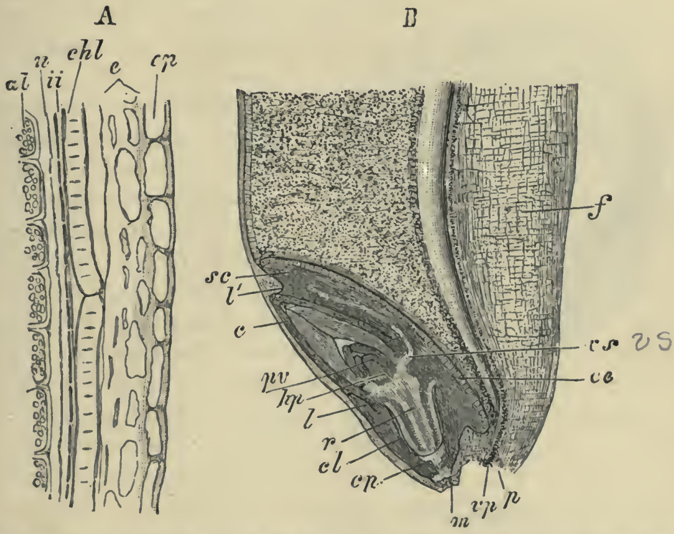

Fig. 346.—Grain of *Triticum vulgare*, the Wheat. *A* Cross-section through the pericarp and testa. Of these, *ep* is the epidermis, *e* the outer layers, and *chl* the chlorophyll-layer, of the pericarp: *ii* remnants of the ovular integument, and *n* the outermost thickened layer of the nucellus; these together constitute the testa: *al* the aleuron-layer of the endosperm (× 240). *B* Median longitudinal section through the lower part of a ripe grain, in the plane of the furrow. At the bottom of this to the left is the embryo: the scutellum, *sc*; *l′* the ligule of the scutellum; *vs* its vascular bundle; *ce* its layer of cylindrical epithelium: *c* the sheath of the plumule (coleoptile); *pv* the growing-point of the stem; *hp* the hypocotyl; *l* the epiblast; *r* the radicle; *cp* the root-cap of the radicle; *cl* the root-sheath (coleorhiza); *m* place of exit of the radicle, corresponding with the micropyle of the ovule; *p* the funicle; *vp* vascular bundle in the funicle; *f* lateral surface of the furrow (× 14). (After Strasburger.)

see 504

o ligule - a little scale at junction of
blade + sheath - ~~Vines~~ K+O II-746

then grow cylindrically: this is the reason why in Palms, in the Maize, and other similar erect stems, there is a diminution in thickness at the lower end. Frequently, however, the primary axis of the plant perishes when it has given rise to lateral shoots.

The arrangement of the leaves is at first alternate: when the stem is well developed this alternate arrangement often passes over into complex spiral arrangements, as in Fritillaria and in Palms, in which plants a crown of leaves is conspicuous. In the Grasses, and a few other families, the phyllotaxis is permanently alternate. A whorled arrangement of the foliage-leaves occurs but rarely.

Edwards 27

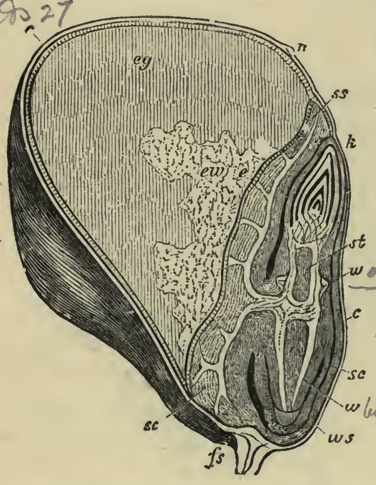

FIG. 347.—Longitudinal section of the grain of *Zea Mais* (× about 6): *c* pericarp; *n* remains of the stigma; *fs* base of the grain; *eg* hard yellowish part of the endosperm; *ew* whiter less dense part of the endosperm; *sc* scutellum of the embryo; *ss* its apex; *e* its epidermis; *k* plumule; *w* (below) the primary root; *ws* the coleorhiza; *w* (above) secondary roots springing from the epicotyl (*st*). (After Sachs.)

The leaves commonly have a well-developed sheathing leaf-base: they may be described as exstipulate, although certain structures, such as the axillary scales (*squamulæ intravaginales*) of Naias, Elodea, Acorus, etc., and the tendrils springing from the petioles of Smilax, have been described as stipules, but without conclusive evidence. The scales of Naias, etc., seem rather to be ligular. The lamina is usually entire, simple in outline, often long and narrow, linear or ensiform, more rarely orbicular, cordate or sagittate. Branched leaves occur only in a few of the Araceæ: the pinnate or palmate leaves of the Palms acquire this form by the splitting of the originally entire laminæ, and the same is the case with the perforated leaves of many Araceæ (see p. 54).

The venation of the leaves is characterized by the fact that the weaker veins do not usually project on the under surface. In linear leaves, and in such as are inserted by a broad base, the stronger veins run almost parallel; in broader ones, *e.g.* Lily of the Valley (*Convallaria majalis*) they describe a curve which is more or less parallel to the margin; the weaker veins usually run at right angles between the stronger ones. In the Scitamineæ and a few other plants, a number of parallel transverse veins are given off at various angles (sometimes acute, and sometimes nearly right angles) from the midrib. Reticulate venation of the leaves is unusual; but it occurs in Aroids, in *Paris quadrifolia*, etc. (see p. 56).

The flower of Monocotyledons consists typically of five alternating and isomerous whorls, two belonging to the perianth, two to the andrœcium and one to the gynæceum. Thus the typical formula is *K*n, *C*n, *A*n + n, *G*n, where n in most cases = 3, more rarely = 2, 4 or 5.

Lateral flowers have a posterior prophyllum; hence the first perianth-leaf is anterior. The perianth-leaves are generally all much alike, and petaloid in both series: sometimes they are all sepaloid (*e.g.* Juncaceæ); more rarely those of the external whorl are sepaloid, those of the internal petaloid (*e.g.* Commelynaceæ, Alismaceæ).

This type is most closely adhered to in the Liliaceæ. The simplest departure from it is exhibited in the suppression of the inner whorl of stamens in the Iridaceæ, and in the inferior position of the ovary. This latter character occurs also in the Scitamineæ and Orchidaceæ, which are further characterized by the zygomorphism of their flowers and the considerable reduction of the andrœcium. Other various and considerable deviations by reduction from the Liliaceous type of flower occur among the Araceæ, and in the Glumales, and Typhaceæ, and in certain water-plants (*e.g.* Naiadaceæ, Lemnaceæ). On the other hand, the deviation may be due to increase in number, more especially of the members of the gynæceum and to some extent of the andrœcium (*e.g.* Alismaceæ).

The principal orders of Monocotyledons may be arranged as follows:—

Sub-class I. SPADICIFLORÆ.

Cohort 1. **Arales.**
  Order 1. ARACEÆ.
  „ 2. LEMNACEÆ.
  „ 3. PANDANACEÆ.
  „ 4. CYCLANTHACEÆ.
  „ 5. TYPHACEÆ.

Cohort 2. **Palmales.**
  Order 1. PALMACEÆ.

Sub-class II. GLUMIFLORÆ.

Cohort 1. **Glumales.**
  Order 1. GRAMINACEÆ.
  „ 2. CYPERACEÆ.

Cohort 2. **Restiales.**
  Order 1. ERIOCAULONACEÆ.
  Order 2. RESTIACEÆ.

Sub-class III. PETALOIDEÆ.

Series i. HYPOGYNÆ.

Sub-series. *Apocarpæ.*

Cohort 1. **Alismales.**
  Order 1. NAIADACEÆ.
  „ 2. JUNCAGINACEÆ.
  „ 3. ALISMACEÆ.
  „ 4. BUTOMACEÆ.

Sub-series. *Syncarpæ.*

Cohort 1. **Commelynales.**
  Order 1. XYRIDACEÆ.
  „ 2. COMMELYNACEÆ.

Cohort 2. **Liliales.**
  Order 1. LILIACEÆ.
  „ 2. JUNCACEÆ.
  „ 3. PONTEDERIACEÆ.

Series ii. EPIGYNÆ.

Cohort 1. **Hydrales.**
  Order 1. HYDROCHARIDACEÆ.

Cohort 2. **Dioscoreales.**
  Order 1. DIOSCOREACEÆ.
  „ 2. TACCACEÆ.
  „ 3. BROMELIACEÆ.

Cohort 3. **Amomales (Scitamineæ).**
  Order 1. MUSACEÆ.
  „ 2. ZINGIBERACEÆ.
  „ 3. MARANTACEÆ.

Cohort 4. **Orchidales.**
  Order 1. ORCHIDACEÆ.

Cohort 5. **Narcissales.**
  Order 1. AMARYLLIDACEÆ.
  „ 2. IRIDACEÆ.

SUB-CLASS I. SPADICIFLORÆ.

Inflorescence usually a spadix with a spathe, but flower sometimes solitary: flowers frequently monosporangiate, sometimes diœcious: perianth, often wanting, never petaloid: anthers usually extrorse, or dehiscing by pores: ovary superior.

Cohort 1. **Arales.** The flowers are small and numerous; the inflorescence a spadix or a panicle with thick branches, commonly enclosed in a greatly developed spathe; the bracts of the individual flowers are frequently wanting; perianth 0, or polyphyllous; the flowers are usually diclinous, but both kinds of flowers frequently occur in the same inflorescence: gynæceum apocarpous or syncarpous: the seeds have a large endosperm: the embryo is straight and minute.

Order 1. ARACEÆ. Flowers monœcious or ☿: perianth 0 or of 4–6 leaves: stamens 1–8, frequently coherent into a synandrium in the ♂ flowers: ovary monomerous, or polymerous and multilocular: fruit a berry: seed sometimes exalbuminous. Mostly tropical.

In many of the genera the flowers are complete and conform to the monocotyledonous type, Kn, Cn, $An + n\ G\ (^{n})$, where n may stand for 2, or 3, as in Acorus (Fig. 348), in which the flowers are exactly typical. In other genera, however, the flowers are reduced in various ways and degrees; not only does the perianth disappear, but the number of the stamens and carpels is frequently diminished. In many ♀ flowers staminodia are present, either in the typical or in a smaller number. An extreme case is offered by those diclinous flowers of which the ♂ consists of only a single stamen (*e.g.* Arisarum), and the ♀ of only one monomerous

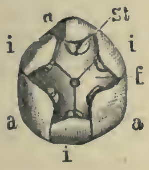

FIG. 348.—Flower of *Acorus Calamus* (mag.): *a* outer, *i* inner perianth: *st* stamens; *f* ovary.

FIG. 349.—Spadix of *Arum maculatum* (nat. size): *f* macrosporangiate, *a* microsporangiate, and *b* rudimentary flowers; *c* the upper club-shaped end of the spadix.

ovary. These much reduced flowers are disposed in regular order on the spadix: thus in Arum (Fig. 349) the numerous ♀ flowers, consisting each of one carpel (Fig. 349*f*), are inserted on the base of the spadix; and the ♂ flowers, each consisting merely of 3–4 stamens, are closely packed higher up on it (Fig. 349 *a*). The upper part of the spadix is covered with rudimentary flowers (*b*, *c*). When, as in this case, the perianth of the true flowers is wholly wanting, the whole inflorescence may assume the aspect of a single flower; but irrespectively of the numerous intermediate forms which are to be found, such a view is untenable when it is borne in mind that here the ovaries are invariably situated below the stamens, while in a flower they are invariably above them.

The usually sympodial stem may be underground, a tuber, or a rhizome, or it may be aerial; in the latter case it often climbs, clinging to trees by means of aerial roots. The leaves are either alternate and distichous or, more often, spiral with a divergence of $\frac{2}{5}$. They are rarely narrow, linear, or ensiform, and commonly consist of leaf-base, petiole, and blade; the venation is reticulate, and the leaf often exhibits a more or less complicated segmentation. Laticiferous sacs or cells (see p. 141) occur in some families of the order, as do also sclerotic cells (see p. 133).

Fam. 1. *Pothoideæ:* without either laticiferous or sclerotic cells: flowers usually ☿, with or without a perianth. This family includes a number of genera, such as Pothos, Anthurium, Acorus. The only member which occurs in Britain is *Acorus Calamus*, the Sweet Flag, which grows on the margins of ponds and rivers: its subterranean rhizome bears long ensiform alternate leaves, crimped at the edges; its flowering-shoot is triquetrous, bearing a terminal spadix which is, however, displaced to one side by the spathe which developes so as to form a continuation of the long axis of the flowering-shoot: the spadix is densely covered with flowers (Fig. 348).

Fam. 2. *Monsteroideæ:* without laticiferous cells, but with sclerotic cells: flowers ☿, mostly without a perianth. *Monstera deliciosa* (sometimes called *Philodendron pertusum*), with perforated leaves, is commonly cûltivated in hot-houses: it comes from Mexico. Scindapsus.

Fam. 3. *Callideæ:* with straight rows of laticiferous cells: flowers usually ☿, with or without a perianth: leaves never sagittate. No member is indigenous in Britain: *Calla palustris* occurs in the marshes of Northern Europe; it has a white spathe and parallel-veined leaves. Symplocarpus. Orontium.

Fam. 4. *Lasioideæ:* with straight rows of laticiferous cells: flowers mono- or ambi-sporangiate, mostly without a perianth: leaves sagittate, often segmented. This family includes a number of typical genera, of which Amorphophallus is the most conspicuous.

Fam. 5. *Philodendroideæ:* with straight rows of laticiferous cells: flowers diclinous, without a perianth: stamens usually connate: leaves generally parallel-veined. *Zantedeschia* (*Calla* or *Richardia*) *æthiopica*, with a white spathe, is commonly cultivated under the name of the Trumpet Lily.

Fam. 6. *Colocasioideæ:* with a net-work of laticiferous vessels: flowers diclinous, mostly without a perianth; stamens connate: leaves with reticulate venation. The genera Alocasia, Colocasia, and Caladium, are commonly cultivated as foliage-plants.

Fam. 7. *Aroideæ:* with straight rows of laticiferous cells: flowers diclinous: usually without perianth. *Arum maculatum*, the Cuckoo-pint or Lords and Ladies, is a British plant, common in wood and hedges; the large green spathe completely envelopes the spadix (Fig. 349). Dracunculus and Arisarum are also European genera.

Fam. 8. *Pistioideæ:* no laticiferous tissue: flowers diclinous, without perianth: microsporangiate flowers numerous and whorled, macrosporangiate flower single, on the spadix.

Pistia Stratiotes, a tropical water-plant, is characterized by having the flowers on the spadix reduced to two, one ♂ flower, and one ♀ flower consisting of a single carpel: the spadix and spathe are adherent. It appears highly probable that the Lemnaceæ, mentioned below, are in fact very simple forms of this family.

Order 2. LEMNACEÆ. Stem leafless. Each inflorescence consists of two ♂ flowers and one ♀ flower borne on a lateral branch of the stem: the ♂ flowers consist of a single stamen, and the ♀ flower of one carpel.

Lemna trisulca, *L.* (*Spirodela*) *polyrhiza*, *minor* and *gibba*, are known as Duck-weed; they are common in tanks and ponds, floating on the water. The stem, which is leafless, is almost flat, resembling a thallus: it bears two rows of branches (Fig. 350), as also roots on its under surface which are suspended in the water. Roots are, however, absent in *Wolffia arrhiza*, which is also devoid of vascular bundles; its flower has no spathe, and it bears only one row of branches: it is the smallest known flowering plant.

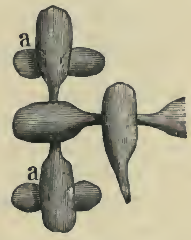

FIG. 350.—Part of a plant of *Lemna trisulca*, seen from above: *a* the young lateral branches (nat. size).

Order 3. PANDANACEÆ. Flowers diœcious, perianth 0: the ♀ flower sometimes consists of a single carpel; or of several carpels forming a multilocular (species of Pandanus) ovary, each loculus containing a single ovule; or of several carpels forming a unilocular (Freycinetia) ovary with numerous parietal ovules; they are closely crowded on the spadix, which becomes a spurious fruit: the ♂ flower has numerous stamens: in the genus Freycinetia, each flower usually has rudiments of the missing reproductive organs.

Pandanus utilis, the Screw-Pine, and other species, form thickets in the tropics, particularly on the banks of rivers. The straight woody stems, which subsequently branch, give off numerous strong adventitious roots which attach them to the soil, and bear crowns of large narrow linear leaves, the margins of which are frequently set with sharp spinous teeth. The tough vascular bundles are used for the manufacture of fabrics. The genus Freycinetia includes a number of shrubs, some of which climb. Tropics of Australasia, and the Malay Archipelago.

Order 4. CYCLANTHACEÆ. Plants of a palm-like habit in Southern and Central America; the diclinous flowers, which usually have a perianth, are disposed on the spadix in regular spirals: ovules many, parietal.

The leaves of *Carludovica palmata* are applied to various purposes, *e.g.* Panama hats are woven of them.

Order 5. TYPHACEÆ. Flowers monœcious; the perianth represented only by scales, or 0. Stamens usually 3. Ovary usually monomerous, containing one ovule. Inflorescence a spadix, without a spathe, elongated or compact.

In Sparganium, the Bur-Reed, the inflorescences are spherical spikes which are borne terminally and laterally in two rows on the upper part of the stem. The lower spikes bear only ♀, and the upper only ♂ flowers; the perianth consists of 3–6 scales; stamens 3–8, free; gynæceum sometimes dimerous with an ovule in each loculus. *Sparganium simplex* and *ramosum* are not rare in ditches.

Typha, the Reed-Mace or Bulrush, bears its flowers on a long terminal spadix; the ♂ flowers are borne directly on the upper and thinner portion of the main axis; on the lower and thicker portion are borne the ♀ flowers, partly on the main axis and partly on very short lateral shoots; the perianth is replaced by long hairs; stamens 1–5, monadelphous. *Typha angustifolia* and *latifolia* occur in bogs and wet places.

Cohort 2. **Palmales.** Order 1. PALMACEÆ. The diœcious or monœcious, rarely monoclinous or polygamous, flowers are inserted, with or without bracts, on the spadix or on the thick axis of a spicate or paniculate inflorescence (Fig. 351): they generally conform to the type $K3$, $C3$, $A3 + 3$, $G^{\underline{(3)}}$: in some instances a larger or a smaller number of stamens are present: anthers sometimes introrse: carpels rarely more or less than 3, either free or connate; when the gynæceum is apocarpous, the ovary is unilocular; when syncarpous, the ovary has from one to three loculi. Each loculus contains, typically, a single basal ovule; but in trimerous ovaries, two of the ovules are generally abortive: frequently not more than one of the carpels (whether the gynæceum be apocarpous or syncarpous) developes into the fruit: the fruit is generally baccate or drupaceous, one-seeded: the seed is large, and the contained endosperm is horny.

Their mode of growth is somewhat various. Most palms bear their leaves closely arranged in a crown at the top of a tall or of a quite short stem, which is clothed for some distance below its apex with the remains of the older withered leaves. But in some genera, *e.g.* Calamus, the stems creep or climb and the leaves are inserted at some distance from each other. The blade of the leaf commonly splits in the course of its growth, assuming a compound palmate or pinnate form (see p. 54). The inflorescence is invested by bracts: there is usually a large bract (spathe) which envelopes the whole inflorescence when young, and other, inner, bracts which either partially invest it or (when branched) its branches.

Palms chiefly inhabit the tropics, particularly the Moluccas, Brazil, and the region of the Orinoco, and the different genera belong exclusively (at least originally) either to the Old or to the New World.

FIG. 351.—Part of the panicle of macrosporangiate flowers of Chamædorea: *s* the thick axis; *a* the external; and *p* the internal whorl of the perianth; *f* ovary (× 3).

Fam. 1. *Coryphinæ*: the gynæceum consists of three free, or but slightly coherent, carpels: fruits 1–3, baccate: the leaf-segments are concave above. *Phœnix dactylifera* (the Date Palm) a native of Asia and Africa, has pinnatifid leaves. Of the three ovaries, one only developes to form the fruit which is known as the Date; the stone of the Date consists of a very thin testa enclosing the large mass of hard endosperm in which the embryo is imbedded. *Chamærops humilis* is a frequently cultivated ornamental plant, with fan-like leaves, which belongs to the Mediterranean region.

Fam. 2. *Borassinæ*: ovary syncarpous, trilocular at its base: fruit 1–3 seeded, smooth, drupaceous, with hard endocarp: leaves fan-shaped, the segments concave above. To this family belong *Hyphæne thebaica*, the Doum Palm of Egypt; and *Borassus flabelliformis*, the Palmyra of India and Africa.

Fam. 1. *Lepidocaryinæ*: ovary syncarpous, trilocular: fruit covered with scales, enclosing a single seed: leaf-segments convex above.

Mauritia is an American genus. Raphia, an African genus, but occurring in America, is one of the few instances in which a genus of Palms is represented in both the New and the Old Worlds: from its leaves "Raphia-bast" is obtained; *R. vinifera* is the Bamboo Palm from which Palm-wine is made in Africa. *Metroxylon* (*Eu-Sagus*) *Rumphii* and *læve*, growing in the Moluccas, are the plants from which Sago is obtained; it consists of the starch-grains obtained from the parenchyma of the trunk. The stems of species of Calamus, in the East Indies, supply Malacca-cane.

Fam. 4. *Ceroxylinæ*: ovary syncarpous, uni- or tri-locular: fruit a berry (sometimes 3 berries by separation of the carpels after fertilisation) or a drupe, 1–3 seeded: leaves pinnate.

Areca Catechu (Fig. 352 *J*) is the Betel-Palm of tropical Asia. *Cocos nucifera* (the Coco-nut Palm) has, as is well known, many uses). The fruit itself is a gigantic drupaceous fruit; the mesocarp is traversed by an immense number of vascular bundles, which are used to make ropes, etc. Inside the excessively hard innermost layer of the pericarp, the endocarp, lies a single large seed. When the fruit is mature, the endosperm forms a layer only a few millimetres in thickness, which lines the hard shell; the rest of the space (the remaining cavity of the embryo-sac) is filled with fluid, known as coco-nut milk. The embryo, which is small, is imbedded in the firm tissue of the endosperm, under the spot where there is a hole (corresponding in position to the style of the single fertile loculus of the ovary) in the endocarp. *Elais guineensis* is the Oil Palm of West Africa; the mesocarp of the plum-like fruit yields the oil.

FIG. 352.—*A* Part of the macrosporangiate inflorescence of *Phœnix reclinata* (nat. size): *B* single macrosporangiate flower: *C* two carpels: *D* floral diagram. *J* Fruit of *Areca Catechu*: one half of the fibrous pericarp has been removed.

Fam. 5. *Phytelephantinæ*: flowers diœcious (Phytelephas) or monœcious (Nipa); in the former genus, the ♀ flowers have numerous staminodes; in the latter the two kinds of flowers are respectively confined to distinct branches of the same spadix, the staminate branches being lateral and amentoid, whilst the carpellary flowers form a cluster at the apex of the main axis: stamens numerous and free (Phytelephas), or three connate (Nipa): perianth sometimes absent (♀ flowers of Nipa): ovary syncarpous, tri-carpellary, one-seeded (Nipa), or of 4–9 carpels (Phytelephas) with as many seeds.

These are low-growing-Palms, Nipa belonging to the East Indies, and Phytelephas to tropical America: the hard endosperm of Phytelephas is known as vegetable ivory.

SUB-CLASS II.—GLUMIFLORÆ.

Flowers ambisporangiate or monosporangiate and then mostly monœcious, usually in heads or spikelets invested by imbricate bracts: perianth absent, or scaly: ovary superior, uni- or multilocular, with one ovule in the loculus: seeds with endosperm.

Cohort 1. **Glumales.** Ovary unilocular: ovule erect.

Order 1. GRAMINACEÆ. True Grasses. The leaves are alternate on the stem, which is known as the haulm; the embryo lies on the side of the endosperm (Figs. 346–7). The usually ambisporangiate flowers generally have the formula $K0$, $C0$, $A3 + 0$, $G1$; they are enclosed by bracts here termed *paleæ*, and are arranged in complicated inflorescences; the monomerous unilocular ovary contains only one ovule; the grain is the fruit, a caryopsis, to which one (the inferior) or, less commonly, both, of the paleæ sometimes adhere, *e.g.* Barley and Oats.

The flower is sessile in the axil of a bract, which is termed the *inferior* or *outer palea*, sometimes also called the *flowering-glume* (Fig. 355 b_1, b_2...), and there is also a bracteole opposite to and somewhat higher than this which is termed the *superior* or *inner palea* (Fig. 355 *ps*). The two paleæ completely enclose the flower.

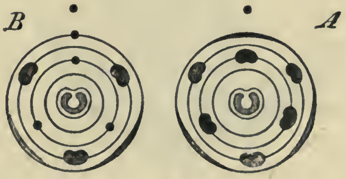

FIG. 353.—Diagrams of Grass-flowers. *A* Bambusa. *B* Common type of Graminaceæ. In *A* there are three, in *B* two lodicules.

Within the inferior palea are usually two small (antero-lateral) scales, the *lodicules* (sometimes only a single anterior one, Melica), and occasionally (*e.g.* Stipa, some Bambuseæ Fig. 353 *A*), there is a third scale situated posteriorly within the superior palea. These lodicules are frequently regarded as rudimentary perianth-leaves (Fig. 353), but it is more probable that they are bracteoles, the two antero-lateral lodicules representing the two halves of a single bracteole, present, as such, in Melica. They grow and become succulent at the time of flowering, thus forcing apart the paleæ and the glumes (Fig. 354). Usually two or more flowers, thus enclosed by paleæ, are present on an axis (Fig. 355 *x*), and constitute the spikelet of the Grass, and beneath the lowest flower there are usually two (or more) bracts which bear no flowers in their axils and are known as the *glumes* (Fig. 355 *g*). Thus a spikelet consists of a main axis bearing two rows of bracts of which the two first and lowest are barren, while the succeeding ones bear each a flower in its axil, and beneath each flower there is also a bracteole (superior palea) belonging to the floral branch itself. The inferior paleæ often have, either at the apex or else borne on the midrib, a spinous process called the *arista* or *awn* (Fig. 355 *gr*).

The number of flowers in each spikelet varies, however, according to the genus; often there is but one, the lowest, with rudiments of others above it; if, however, only one of the upper flowers is developed, then the lower paleæ bear no flowers in their axils and are regarded as glumes, several being therefore present in such a case. The spikelets themselves are in many genera, *e.g.* Rye and Wheat (Fig. 356 *B*), arranged in two rows on a main axis; the inflorescence may then be designated a compound spike (see p. 491); in most of the other genera the main axis of the inflorescence bears lateral branches which are slender, of various length, and often branched again, and which bear the terminal spikelets; in this way a panicle is formed, as in the Oat (Fig. 356 *A*). This may be either loose and spreading, with long lateral branches, or compressed, with very short branches, *e.g.* Alopecurus. The

FIG. 354.—Single-flowered spikelet of *Panicum miliaceum* (mag.); C_2 and C_3 second and third glumes: *D* inferior palea: *E* superior palea.

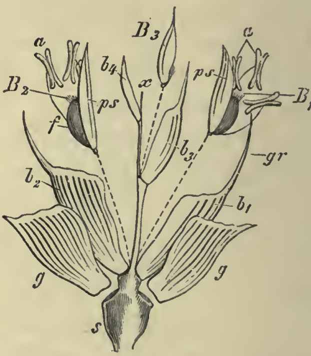

FIG. 355.—A spikelet of Wheat dissected (mag.): *x* axis of the spikelet; *g* glumes; b_1 b_2 b_3 b_4 inferior paleæ bearing (*gr*) the awn; b_4 is sterile. B_1 B_2 B_3 the flowers raised (as indicated by the dotted lines) out of the axils of the inferior paleæ; *ps* superior paleæ; *a* anthers; *f* ovaries.

position of the branches of the panicle is more or less bilateral; dorsiventral, when (*e.g.* Festuca) the branchlets of the main branches of the panicle all arise on the same side (unilateral or secund panicle).

The andrœcium consists commonly of one (Fig. 353 *B*) or two (*A*) whorls of 2–3 stamens; when there is but one whorl of stamens, it corresponds to the outer whorl in those flowers in which two whorls are present. Sometimes (*e.g.* Luziola, Ochlandra, Pariana) the stamens are numerous (about 18–20), or there may be but one or two. When there are normally only two stamens, they are usually situated in the median plane (*e.g.* Anthoxanthum), sometimes in the lateral plane (*e.g.* Coleanthus); but where this is the result of suppression (Diarrhena, Orthoclada) they are postero-lateral, the anterior stamen being suppressed: when there is only a single stamen, this is generally the anterior stamen (*e.g.* species of Festuca and Andropogon), the two postero-lateral stamens being suppressed.

The monomerous gynæceum consists of a single median carpel (Fig. 353), bearing 1–3 styles (see p. 524): the single, somewhat campylotropous ovule is sessile on the ventral suture of the carpel.

The stem is generally characterised by swollen or tumid nodes, to which the sheathing leaf-bases contribute. The long internodes are hollow: the sheathing leaf-bases are largely developed, and frequently extend over several internodes. A membranous ligule is developed at the junction of leaf-base and lamina (see p. 48; Fig. 28).

The more common Grasses are classified as follows:—

Series *A*. PANICOIDEÆ: spikelet one-flowered, or sometimes two-flowered and then the lower flower is imperfect; articulated so that it falls off entire after flowering; no prolongation of the axis beyond the flower.

Tribe 1. *Paniceæ*: spikelets dorsally compressed, in compound spikes: glumes 3, of which the lowest is the smallest: inferior palea without an awn.

Panicum glabrum (*Digitaria humifusa*), *P.* (*Echinochloa*) *Crus-galli*, and *P.* (*Setaria*) *viride* occur occasionally on cultivated land. *P. miliaceum* yields Millet.

Tribe 2. *Maydeæ*: the diclinous flowers are in distinct spikelets; the two kinds of spikelets usually form distinct inflorescences, but sometimes they occur in different parts of the same inflorescence: the lowest glume is the largest.

Zea Mais, the Maize Plant, cultivated in warm countries, is a native of Tropical America: the ♂ spikelets form a loose panicle at the apex of the haulm, and the ♀ flowers are borne laterally on a thick spadix, which is ensheathed by leaves. Coix belongs to this tribe.

Tribe 3. *Andropogoneæ*: flowers monœcious or polygamous: glumes 3, of which the lowest is the largest.

Saccharum Officinarum, the Sugar-cane, is a native of the East Indies. *Andropogon Sorghum*, in different varieties (*vulgaris*, *Durra*, etc.), yields a kind of Millet seed: the flour of this is known in Arabia and India as Durra.

Tribe 4. *Oryzeæ:* spikes laterally compressed: glumes 2–4, often represented only by bristles: stamens generally 6. *Oryza sativa* is the Rice-plant, from the East Indies; cultivated in marshy regions of Southern Europe. *Leersia oryzoides*, the Cut-Grass, is found in ditches in the South of England.

Series *B*. Pooideæ: spikelet one- or many-flowered, with distinct internodes between the flowers: when one-flowered, the axis of the spikelet is prolonged beyond the flower: the ripe fruits fall, leaving the glumes behind.

Fig. 356.—*A* Panicle of Oat, *Avena sativa*: *s* main axis; *s′* lateral axes; *a* spikelet (⅓ nat. size). *B* Spike of Wheat: *s* axis; *g* the depressions in which the spikelets (*a*) lie. These are removed at the lower part.

Tribe 5. *Phalarideæ:* spikelets pedicillate in panicles, laterally compressed, 1-flowered: glumes 4, the inner pair being smaller. *Phalaris arundinacea*, the Reed-Grass, is common on the banks of streams, etc.: a variety with white-streaked leaves is cultivated in gardens. *Anthoxanthum odoratum*, Vernal-Grass, which has only two stamens and a paniculate inflorescence, is common in meadows: it gives the peculiar odour to fresh hay.

Tribe 6. *Agrostideæ:* spikelets 1-flowered, in panicles: glumes 2.

In Agrostis, the Bent-Grass, the axis of the spikelet is glabrous, or it bears short hairs; *A. vulgaris* and *alba* are common in meadows: *Apera Spica Venti* is common in fields: in Calamagrostis, the Small Reed, several species of which occur on the banks of rivers and in woods, the axis of the spikelet is covered with long hairs. *Stipa pennata*, the Feather-Grass, has a long hairy awn. *Milium effusum*, Millet-Grass, without an awn, is common in woods. Amongst the forms with dense cylindrical panicles, Alopecurus, the Fox-tail Grass, has the glumes coherent at the base, and one rudimentary palea. Phleum, the Cat's-tail Grass, has free glumes and two distinct paleæ. *Phleum pratense* is commonly known as Timothy-Grass.

Tribe 7. *Aveneæ:* the paniculate, or rarely spicate, spikelets consist of several (usually two) flowers one of which is sometimes ♂; the glumes (or one of them at least) are as long as the whole spikelet, longer than the inferior paleæ, which usually have a long twisted or bent awn.

Avena, the Oat-Grass, has loose panicles, and a two-toothed inferior palea; of this genus there are many species; *A. fatua* (Wild Oats, or Havers), *pratensis* and *pubescens*, are common in cornfields and meadows. The following species are cultivated: *A. sativa*, the Oat (Fig. 356 *A*), with its panicles in various planes; *A. orientalis*, with its panicles in one plane; *A. strigosa*, with a hairy floral axis; and *A. nuda*, the spikelets of which usually consist of three flowers. *Trisetum* (*Avena*) *flavescens*, the yellow Oat-Grass, with a free fruit, occurs in pastures. *Aira* (*Deschampsia*) *cæspitosa*, and *flexuosa*, Hair-Grasses, have truncate inferior paleæ, and are common in meadows and woods. Holcus, the Honey-Grass, has spikelets consisting of two flowers, the upper of which is usually ♂, and the leaf-sheaths are covered with silky hairs; it is common in damp meadows. In Arrhenatherum, the False Oat-Grass, the lower of the two flowers is ♂.

Tribe 8. *Festuceæ:* the spikelets are usually many-flowered, and the glumes shorter than the inferior paleæ which either have no awn or a straight terminal awn. Melica, the Melic-Grass, has sometimes spikelets consisting of a single flower only: the glumes are long; it is common in woods. *Molinia cærulea* has a very long haulm, consisting for the most part of a single internode; its spikelets are in loose purplish panicles; it occurs on moors. Briza, the Quaking-Grass, has spikelets which are compressed laterally and are cordate at the base; it is common in meadows. *Koeleria cristata* has dense panicles; it is common in dry meadows. *Dactylis glomerata*, the Cock's-foot Grass, has dense panicles divided into parts which have longer stalks; it is common in meadows. *Poa pratensis*, *trivialis*, etc. (Meadow-Grass), are common in meadows; their spikelets are compressed laterally; the glumes have a sharp keel; *P. annua* is common by the roadside. Other Meadow-Grasses are *Glyceria aquatica* and *fluitans*, with obtuse unequal glumes, and a lower palea with 5–7 prominent parallel veins, growing in ditches; and *Schlerochloa maritima*, *distans*, etc., growing in salt-marshes and by the sea-shore, with acute unequal glumes. In all the Meadow-Grasses, the fruit is free from the paleæ. *Festuca elatior*, and others, the Fescue Grasses, are common in meadows. Bromus, the Brome-Grass, of which there are several species, is common in fields (*B. secalinus*), in meadows (*B. racemosus* and others), by the roadside (*B. sterilis* and *mollis*). Brachypodium, with shortly-stalked spikelets in a simple raceme, and unequal glumes, is common in woods (*B. sylvaticum*) and on heaths (*B. pinnatum*). In Phragmites the axis of the spikelet is covered with long silky hairs; *Phragmites communis*, the Reed, occurs abundantly in marshes. *Sesleria cærulea*, the Moor-Grass, has laterally compressed spikelets in dense panicles. Gynerium, the Pampas-Grass, also belongs here; it is diœcious. The upper flowers in the spikelets of plants belonging to this tribe are often unisexual, and ♂; Phragmites is peculiar in that the lower flower of the spikelet is ♂.

Tribe 9. *Chlorideæ:* spikelets laterally compressed, usually 1-flowered, sessile, in compound spikes: glumes 2. *Cynodon Dactylon*, the Dog's-tooth Grass, is often abundant on waste ground. *Spartina stricta* occurs in salt-marshes.

Tribe 10. *Hordeæ:* spikelets solitary, or 2 or 3 together, 1- or many-flowered, situated in depressions on the main floral axis nearly always in two opposite rows, forming the so-called spike: glumes 1–2. In Lolium, the Rye-Grass (*L. perenne*, Darnel, is common everywhere), the posterior surface (that is, the middle line of the posterior glume) is directed towards the main axis, and this glume is usually rudimentary. In all the other genera the side of the spikelet is directed towards the main axis, and there are two glumes. In Agopyrum, the paleæ adhere and fall off with the fruit: *A. repens*, the Couch-Grass, is common everywhere, and is a troublesome weed on account of its spreading rhizome. *Secale cereale*, the Rye, has 2-flowered spikelets and narrow awl-shaped glumes. In *Nardus stricta*, the Mat-Grass, the two rows of spikelets converge laterally; the glumes are rudimentary; there is but one stigma; the leaves and haulms are rough; it grows on moors. Triticum, the Wheat, has 3- or more flowered spikelets, with ovate glumes. Three species are cultivated, *T. monococcum*, *T. sativum*, and *T. polonicum*; in the first species the terminal spikelet is abortive. The following varieties of *T. sativum* are cultivated; *T. vulgare*, the common Wheat, with long glumes, which have no keel, and *T. turgidum*, English Wheat, with short keeled glumes; *T. compactum*, the Dwarf Wheat, with short, stout spikelets; and *T. durum*, the Hard Wheat, known by its long rigid awns; all these varieties have a wiry floral axis (hence sometimes described as *T. sativum tenax*), and the fruit easily falls out of the glumes, and in all but *T. durum* there are awned and un-awned (beardless) forms: *T. Spelta*, the Spelt, which has an almost quadrangular spike, and *T. dicoccum*, with a compact spike, have a brittle floral axis, and the fruit is firmly enclosed by the glumes. In all the species the length of the awn varies very much. Hordeum, the Barley, has 3 single-flowered spikelets inserted together in one depression on the floral axis. *H. murinum* is common on the roadside and on walls. The following varieties of *H. sativum* are cultivated: *H. vulgare* and *H. hexastichum*, with only fertile spikelets; in the latter species the spikelets are all equally distant, and are therefore arranged in six rows; in the former species the median spikelets are nearer together, and the lateral ones more distant, so that they are described as being in four rows: further, *H. distichum* is the two-rowed Barley, the lateral spikelets of which are ♂, so that the fruits are arranged in two rows. The fruit usually adheres to the palea; the embryo has no epiblast. The genus Elymus, the Lyme-Grass (*E. arenarius*, British) belongs to this tribe, as also Pariana, a tropical genus remarkable for its numerous stamens.

Tribe 11. *Bambuseæ:* spikelets 2- or many-flowered, rarely 1-flowered, in racemes or panicles, clustered at the nodes of the branches of the inflorescence: glumes 2 or many, becoming larger upwards, but shorter than the nearest palea (see Fig. 353 *A*): stamens generally 6. Large Grasses, known as Bamboos, having perennial aerial shoots with often shortly petiolate leaves, growing mostly in the Tropics. The most familiar genera are Arundinaria and Bambusa.

Order 2. CYPERACEÆ. The leaves are arranged in three rows on the stem: perianth 0, or of 3–6 or more bristles or scales: the andrœcium consists typically of two trimerous whorls, though one whorl (the inner) is absent in some genera: the gynæceum is typically trimerous, though it is sometimes dimerous: ovary unilocular: ovule erect, anatropous; the embryo is enclosed in the endosperm.

Tribe I. *Scirpoideæ:* flowers ☿; perianth 0, or of bristles: glumes distichous: the odd carpel is anterior. The spikelets are often arranged so as to form spikes, panicles, umbels, or capitula: the flower has the formula $K3$, $C3$, $A3+0$ or 3, $G^{\underline{(3)}}$.

Cyperus, the Galingale, has many-flowered compressed spikelets with deciduous bracts or glumes: Schœnus, the Bog-Rush, has few-flowered (1–4) spikelets with persistent glumes: *C. longus* and *fuscus*, and *S. nigricans*, occur in England. *Cyperus Papyrus* (*Papyrus Antiquorum*) is an Egyptian species from which the Papyrus of the ancients was made.

Scirpus, the Club-Rush, has a bristly perianth, cylindrical spikelets, and the glumes are imbricate on all sides; in some species the spikelets are solitary, as in *Scirpus cæspitosus*, in others there are lateral spikelets, in addition, on short stalks, as in *S. lacustris* (the true Bulrush), or on long stalks, as in *S. sylvaticus*. *Eriophorum polystachium* and other species (Cotton-grass) are common on boggy moors; the hairs of the perianth, after flowering, grow to a considerable length.

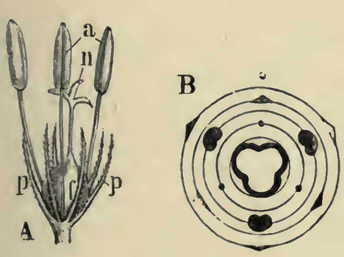

FIG. 357.—*A* Flower of Scirpus (magnified): *p* the bristly perianth; *a* the three stamens; *f* the ovary: *n* the three stigmata. *B* Its floral diagram.

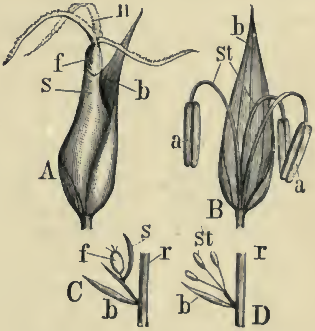

FIG. 358.—Flower of Carex (mag.). *A* ♀ flower with (*b*) bract (glume); *s* second bract (utriculus); *f* ovary; *n* stigma. *B* ♂ flower: *st* the three stamens; *a* anthers. *C* Diagram of the ♀ and (*D*) of the ♂ flower: *r* axis of the spike; *b* bract (glume); *s* second bract.

Tribe 2. *Caricoideæ:* spikelets cylindrical; flowers monosporangiate; perianth 0.

These plants have diclinous (sometimes diœcious) flowers. In the genus Carex the ♂ flowers have the formula $K0$, $C0$, $A3+0$, $G0$; they are situated in the axils of bracts (glumes) (Fig. 358 *B* and *D*) and form simple spikes. The ♀ flowers have the formula $K0$, $C0$, $A0+0$, $G^{\underline{(3)}}$ or $^{\underline{(2)}}$ and are not sessile in the axils of the glumes (*b* in Fig. 358 *A* and *C*), but a short branch springs from the axil of each of these leaves bearing a second bract (*s* in the Fig.) and it is in the axil of this second bract that the ♀ flower, which consists of a trimerous, or more rarely, dimerous (in *Carex dioica* and *pulicaris*, etc.) ovary, is situated. The second bract increases greatly and invests the fruit (and the short branch which sometimes projects beyond the fruit as a *seta*), forming the so-called *utriculus*: this structure has been regarded as a perianth, and termed the *perigynium*. In Kobresia (Elyna) the second bract is not tubular, and therefore does not completely invest the ovary. In consequence of there being a second bract, the odd carpel of the trimerous gynæceum is posterior: when the gynæceum is dimerous, the two carpels are lateral.

The genus Carex, the Sedge, contains numerous species which grow mostly in damp localities; they have stiff leaves with sharp or saw like edges. Only a few of them are diœcious (*C. dioica*, *scirpoidea*): in most the ♂ and ♀ inflorescences occur on the same axis. In one large section of them the two kinds of flowers occur on the same spike which is either ♂ at the base and ♀ at the top, or *vice versâ*. When this is the case the axis bears either only one terminal spike, as in *Carex pulicaris* and *C. pauciflora*, or several spikes forming a capitulum at the apex, as in *C. cyperoides*, or a spike or a panicle, as in *C. muricata*, *arenaria*, and *paniculata*. In a second section, on the other hand, each spike is monosporangiate, and then the ♂ spike is almost always terminal on the axis and the ♀ lateral, as in *Carex acuta*, *glauca*, *præcox*, *digitata*, *flava*, and *paludosa*.

Cohort 2. **Restiales.** Ovary usually multilocular; a single orthotropous and suspended ovule in each loculus; hence in the seed the radicle of the embryo is directed away from the hilum (*enantioblastic*). Flowers monosporangiate, rarely ambisporangiate, with bracts: floral formula $K3$, $C3$, $A3+3$, $G(3)$, but occasionally some of the members are wanting.

Order 1. ERIOCAULONACEÆ. Flowers monosporangiate, in capitula, often monœcious in the same capitulum, or rarely diœcious: stamens generally in two whorls, anthers generally bilocular: ovary 2–3-locular: seed ribbed.

Eriocaulon septangulare, the Jointed Pipewort, occurs in the Hebrides and on the west coast of Ireland: other genera mostly tropical: generally marsh-plants.

Order 2. RESTIACEÆ. Flowers usually diœcious by suppression, in spikes: only the inner whorl of stamens is present, anthers generally bilocular: ovary 1–3-locular: seed smooth or tuberculate.

These are grass-like sub-tropical plants living in the southern hemisphere. This order includes the group Centrolepidaceæ (Desvauxiaceæ, *Lindl.*); in these the perianth is much reduced, the ♂ flower probably has only one stamen, and the ♀ one or more monomerous ovaries.

SUB-CLASS III. PETALOIDEÆ.

Flowers ambisporangiate, rarely monosporangiate; perianth rarely wanting, usually biseriate, the corolla usually petaloid, and sometimes the calyx also.

SERIES I. HYPOGYNÆ.

Ovary superior.

Sub-series. Apocarpæ.

Gynæceum more or less completely apocarpous.

Cohort 1. **Alismales.** Marsh- or water-plants; flowers frequently monosporangiate; seeds without endosperm.

Order 1. NAIADACEÆ. Perianth 0, or of 2–4 segments; stamens 1–4: ovaries 1–4, with usually a single erect or suspended ovule. Water-plants.

Fam. 1. *Naiadeæ.* Flowers monosporangiate.

In the genius Naias the flowers are solitary or in spikes, and are diœcious: perianth of one or two gamophyllous series: ♂ flowers with 1 stamen, ♀ flowers with 1 carpel: ovule erect. *N. flexilis* is the only British species.

Fam. 2. *Zostereæ.* Flowers monosporangiate.

In Zostera, the Grass-wrack, the flowers are monœcious, and without a perianth; they are borne in two rows on one side of a flattened spike; stamen 1, carpel 1. *Zostera marina* and *nana* are the British species living in the brackish water of estuaries. Phyllospadix, a North American (west-coast) genus, also belongs to this family: it is diœcious.

Fam. 3. *Zannichellieæ.* Flowers monosporangiate.

In Zannichellia, the Horned Pondweed, the monosporangiate flowers are monœcious, and are solitary or in spikes: ♂ flower, perianth 0, stamen 1; ♀ flower, perianth bell-shaped, carpels 4–6. *Z. palustris* is the only British species. Althenia, the other genus, is sometimes diœcious.

Fam. 4. *Cymodoceæ.* Marine. Flowers monosporangiate, diœcious: perianth 0: ♂ flower consists of two connate stamens; ♀ flower of two adjacent monomerous ovaries, each bearing a style which branches into two stigmata; ovule single, suspended, orthotropous.

To this family belongs the genus Cymodocea (with the sub-genera Phucagrostis, Physoschœnus, and Amphibolis); widely distributed on tropical and sub-tropical sea-coasts.

Fam. 5. *Posidonieæ.* Marine. Flowers monosporangiate, sometimes ☿, in cylindrical compound spikes, the upper flowers of which are ♂: perianth 0: the ♂ flower consists of 3 stamens, the ♀ flower of a single carpel.

To this family belongs the single genus Posidonia; *P. oceanica* inhabits the shores of the Mediterranean. *P. australis* the shores of temperate Australia. In Zostera, Posidonia, and Cymodocea, the pollen is filiform or confervoid (see p. 520).

Fam. 6. *Potamogetoneæ.* Flowers ☿.

In Potamogeton, the Pondweed, the flowers are in spikes: general formula $P0$, $A2+A2$, $G\times 4$: the extrorse stamens have a broad leafy connective. This genus is represented in Britain by many species: in some (*P. pusillus*) the stem bears only submerged leaves which are narrow and linear; in others the leaves are somewhat broader (*P. densus*), and in others again it bears a few broad leaves which float on the water (*P. natans*).

In Ruppia, the Tassel Pondweed, the flowers are generally two on a spike; formula $P0$, $A2$, $G4$. *R. maritima* is the British species.

Fam. 7. *Aponogetoneæ.* Flowers ☿, in spikes: perianth of 2 or 3 petaloid leaves: general floral formula $P2\text{–}3$, $A6$, $G3$, but sometimes (as in *Aponogeton distachyus*) there may be six stamens and many carpels: ovules marginal, anatropous, either numerous, or as few as three.

This family includes the single genus Aponogeton, an aquatic plant inhabiting the tropical and temperate regions of Asia, Africa, and Australia.

A. (*Ouvirandra*) *fenestralis* is remarkable for the peculiar structure of its leaves (see p. 55).

Order 2. JUNCAGINACEÆ. Flowers sometimes diœcious; both perianth-whorls are sepaloid and inconspicuous; anthers extrorse; carpels sometimes coherent; the outer whorl of carpels is occasionally abortive; ovules 1–2, anatropous, embryo straight.

Triglochin palustre, the Arrow-Grass, is common in marshes and on the margin of pools: carpels coherent till mature. The flowers are disposed spirally in a long loose spike without bracts. *Scheuchzeria palustris* is rarer; it occurs in bogs; the flowers are set in the axils of distichous bracts: carpels free. The other genera are, Tetroncium, from the Straits of Magellan, with diœcious flowers; and Lilæa, from the mountains of North and South America, which is polygamous, having ♂, ♀, and ☿ flowers.

FIG. 359.—Diagram of the Flower of Triglochin.

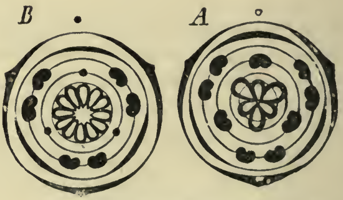

FIG. 360.—Floral diagrams. *A* of Butomus. *B* Of Alisma.

Order 3. ALISMACEÆ. Flowers sometimes monœcious; floral formula $K3$, $C3$, $A3^2+0$ or 3, or ∞, $G3+3$ or ∞: perianth heterochlamydeous; the sepals are often coherent at the base; the petals are white or violet; anthers extrorse or introrse; carpels sometimes partially coherent; ovules 1–3, campylotropous, embryo curved.

Alisma Plantago (Water Plantain, Fig. 360 *B*), has the floral formula $K3$, $C3$, $A3^2+0$, $G6$ or more; the numerous, monomerous, one-seeded ovaries are crowded on the broad receptacle. The main axis of the inflorescence bears whorls of branches which have a helicoid ramification. It is rather common in damp spots. *Damasonium stellatum*, the Star-fruit, is found in ditches in the South of England : it has two-seeded ovaries.

Sagittaria sagittæfolia, the Arrowhead, has monœcious flowers with the formula $K3$, $C3$, ♂ $A\ \infty$, ♀ $G\underline{\infty}$. The flowers are disposed in trimerous whorls, the ♂ in the upper and the ♀ in the lower whorls. The anthers are extrorse. The ovaries, which are very numerous and one-seeded, are inserted on a fleshy receptacle. Only the sagittate leaves and the inflorescence appear above the water.

Order 4. BUTOMACEÆ. Flowers never monosporangiate; general floral formula the same as in Alismaceæ ; anthers introrse ; carpels distinct ; ovules numerous, with superficial placentation ; embryo straight or curved.

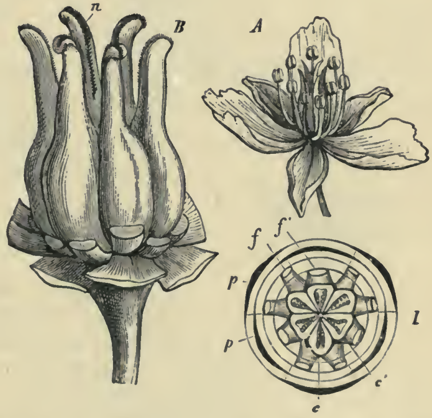

FIG. 361.—*Butomus umbellatus*. *A* Flower (nat. size). *B* Gynæceum (mag.); *n* stigmata. *I* Diagram: *p p* perianth; *f* stamens of the outer whorl duplicate: *f'* stamens of the inner whorl; *c* outer, and *c'* inner whorl of carpels. (After Sachs.)

Butomus umbellatus is the Flowering Rush (Figs. 360 *A*, 361). The flowers, which have violet petals, have the following formula: $K3$, $C3$, $A3^2+3$, $G^{\underline{3+3}}$; they are arranged in an umbellate helicoid cyme at the apex of the scape, which is about 3 feet high ; this and the leaves, which are of about the same length, spring from an underground rhizome. The ovules, which are numerous, are borne on the inner surface of the carpels (Fig. 338 *C*): the embryo is straight.

The other genera all have a curved embryo : in Tenagocharis (Butomopsis) there are nine stamens and six carpels : in Hydrocleis there are indefinite stamens (some sterile) and six carpels : in Limnochari both the stamens (some sterile) and carpels are indefinite.

Sub-series. Syncarpæ.

Gynæceum syncarpous.

Cohort 1. **Commelynales.** Perianth heterochlamydeous ; seeds with starchy endosperm.

Order 1. XYRIDACEÆ. Herbaceous sedge-like plants ; floral formula $K3$, $C3$, $A3+0$, $G^{\underline{(3)}}$; anthers extrorse; ovary usually unilocular, with parietal placentation.

These plants (Xyris, Abolboda) inhabit swamps in tropical or sub-tropical regions.

Order 2. COMMELYNACEÆ. Herbaceous plants; general floral formula $K3$, $C3$, $A3+3$, $G^{\underline{(3)}}$, but the number of stamens varies in the genera; anthers usually introrse; ovary usually trilocular.

These are mostly tropical plants. Species of Commelyna and Tradescantia are cultivated as ornamental plants.

Cohort 2. **Liliales.** Perianth homochlamydeous, usually petaloid; seeds with endosperm; general floral formula $K3$, $C3$, $A3+3$, $G^{\underline{(3)}}$.

Order I. LILIACEÆ. The flowers conform generally to the above formula, but 3 is replaced sometimes by 2 or 4: they are not zygomorphic: endosperm oily; fruit a capsule or a berry. Mostly rhizomatous or bulbous plants: rarely trees or shrubs.

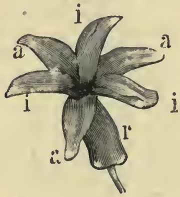

FIG. 362.—Flower of the Hyacinth: *a a a* the three outer; *i i* the three inner segments of the perianth, which is tubular at the lower part (nat. size).

Sub-order 1. LILIOIDEÆ, with a loculicidal capsule, introrse anthers, and united styles. Bulbous plants.

The family *Tulipeæ* includes the following genera: Lilium, Fritillaria, Tulipa, Erythronium, Lloydia, Calochortus (with septicidal capsule).

Many species are cultivated. *Lilium candidum* is the white Lily; *L. bulbiferum*, producing bulbils in the axils of the upper leaves; *L. Martagon*, the Turk's Cap Lily; *L. tigrinum*, the Tiger-Lily; *L. speciosum*, *auratum*, etc. *Fritillaria imperialis* is the Crown Imperial, the flowers of which are surmounted by a crown of leaves. *Tulipa Gesneriana* is the Tulip. *Erythronium Dens-Canis* is the Dog-Tooth Violet. Calochortus is the Mariposa Lily of California. The following occur wild in Britain: *Lilium Martagon; Tulipa sylvestris*, wild Yellow Tulip; *Fritillaria Meleagris*, the Snake's Head; *Lloydia serotina*.

The *Scilleæ* includes the following genera amongst others: Galtonia, Hyacinthus, Muscari, Chionodoxa, Lachenalia, etc., in which the segments of the perianth cohere more or less (Fig. 362); Scilla, Camassia, Ornithogalum, etc., with free perianth-leaves. The following occur wild in Britain: *Hyacinthus non-scriptus*, the Blue Bell; *Muscari racemosum*, the Grape-Hyacinth; *Scilla verna* and *autumnalis; Ornithogalum nutans*, the Star of Bethlehem.

Sub-order 2. MELANTHIOIDEÆ or COLCHICOIDEÆ, with a usually septicidal capsule, usually extrorse anthers, and separate styles. Mostly rhizomatous plants.

Not many genera are common in cultivation; among these Gloriosa, Uvularia, and Veratrum may be mentioned; *Veratrum album* and *nigrum* have broad ovate leaves.

Tofieldia palustris, the Scottish Asphodel, has ensiform radical leaves; the flowers, which are pale green, are disposed in a raceme on a scape; it occurs

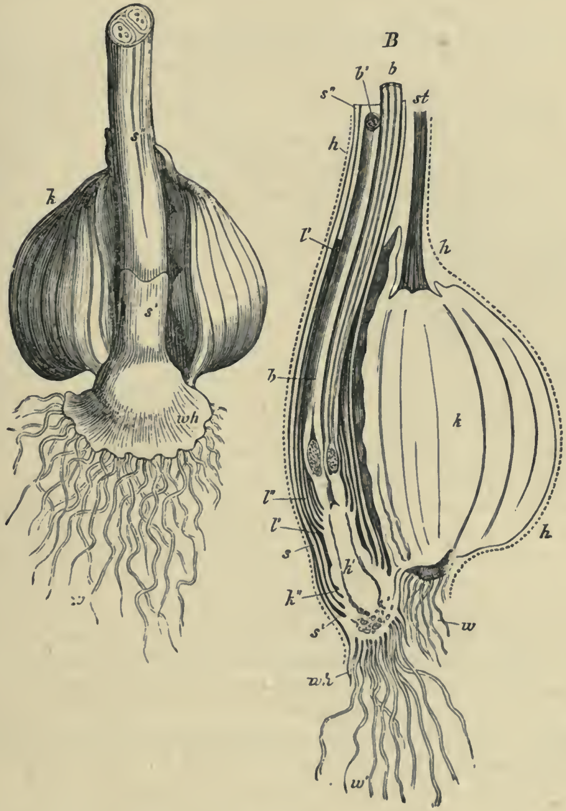

Fig. 363.—The underground part of a flowering plant of *Colchicum autumnale*. *A* Seen in front; *k* the corm; *s' s''* cataphyllary leaves embracing the flower-stalk; *wh* its base, from which proceed the roots, *w*. *B* Longitudinal section: *h h* a brown membrane which envelops all the underground parts of the plant; *st* the flower and leaf-stalk of the previous year which has died down, its swollen basal portion (*k*) only remaining as a reservoir of food-materials for the new plant now in flower. The new plant is a lateral shoot from the base of the corm (*k*), consisting of the axis, from the base of which proceed the roots (*w*), and the middle part of which (*k'*) swells up in the next year into a corm, the old corm (*k*) disappearing; the axis bears the sheath-leaves (*s s' s''*) and the foliage-leaves (*l' l''*); the flowers (*b b'*) are placed in the axils of the uppermost foliage-leaves, the axis itself terminating amongst the flowers. (After Sachs.)

in Scotland, in wet places on mountains, but it is rare. *Narthecium ossifragum*, the Bog-Asphodel, somewhat resembles Tofieldia, but the flowers are yellow and the capsule is loculicidal; common in Scotland and in the north of England.

The *Colchiceæ* are bulbous plants and have introrse anthers. *Colchicum autumnale* is the Autumn Crocus or Meadow Saffron; when it is flowering in the autumn, the stem is underground; it is at this time short and slender (Fig. 363 *k*′), attached laterally to the corm of the previous year's growth (*k*), and bears a few imperfectly developed leaves (*l*′ *l*″) as well as one or two flowers (*b*′ *b*″): the ovaries of the flowers are also subterranean; the six leaves of the perianth cohere and form a tube of some centimetres in length, which grows far beyond the ovaries and above the surface of the soil, terminating in a petaloid six-partite limb; the stamens are attached in the upper portion of the tube. In the spring the underground stem swells at its base (k^r) into a corm, and grows upwards, so that the developing leaves (*l*′ *l*″) and the capsule rise above ground; a lateral shoot is formed at its base, which, in the autumn, produces flowers, and this repeats the process.

Sub-order 3. ASPHODELOIDEÆ; rhizomatous plants, with usually radical leaves, but the leaves are sometimes borne on an aerial rarely branched stem; inflorescence usually a terminal spike or raceme: perianth-leaves free or connate; anthers introrse; fruit capsular.

Asphodelus, Eremurus, Anthericum, Chlorophytum, Bowiea, Hemerocallis, Phormium (*Phormium tenax* is the New Zealand Flax), Kniphofia, Aloë, Gasteria, and Xanthorhæa are cultivated. The only British species is *Simethis bicolor* in the south of England.

Sub-order 4. ALLIOIDEÆ; generally bulbous plants: inflorescence umbellate. more or less completely enclosed by two or more bracts.

Agapanthus, Nothoscordum, Milla, Brodiæa, and Allium are the more commonly cultivated genera. Of Allium, several species are in cultivation for culinary purposes, as *A. Cepa*, the Onion; *A. ascalonicum*, the Shalot; *A Schoenoprasum*, Chives; *A. Porrum*, the common Leek; *A. sativum* (*vulgare*), Garlic. Some species (Wild Garlic) are wild in Britain, such as *A. oleraceum*, *vineale*, *ursinum*, and *triquetrum* in Guernsey. The leaves of the various species of Allium are generally tubular and hollow; the flowers are disposed in spherical heads or umbels; bulbils are occasionally produced among the flowers. *Gagea lutea* is also British.

Sub-order 5. DRACÆNOIDEÆ, stem erect, usually arborescent, with secondary growth in thickness (see p. 205).

Species of Yucca are commonly cultivated in gardens; Cordyline and Dasylirion in greenhouses. *Dracæna Draco* is the Dragon's Tree of the Canary Islands, yielding a red gum-resin (Dragon's-blood).

Sub-order 6. ASPARAGOIDEÆ, with a subterranean rhizome bearing aerial leafy stems: fruit baccate.

Asparagus officinalis is the Asparagus; the young shoots, which spring from the underground rhizome, are eaten. *Convallaria majalis* is the Lily of the Valley. *Maianthemum bifolium* has a dimerous flower. Polygonatum is Solomon's Seal. *Ruscus aculeatus* (the Butcher's Broom), and other species, are small shrubs, with leaf-like branches (phylloclades, see p. 45), on which the diclinous flowers are borne in the axils of minute leaves. *Paris quadrifolia* (Herb Paris) is poisonous: the flowers are tetramerous, or exceptionally trimerous or pentamerous: they are terminal, and the stem beneath bears four (or three or five) leaves in a whorl beneath the flower (Fig. 364); the venation of the leaves is reticulate. Trillium, the Wood Lily, is frequently cultivated. *Aspidistra lurida* is the Parlour Palm.

Maianthemum bifolium, *Paris quadrifolia*, *Ruscus aculeatus*, *Convallaria majalis*, *Polygonatum verticillatum*, *multiflorum*, and *officinale*, are wild in England.

Sub-order 7. SMILACOIDEÆ, scrambling shrubs, having 3–5 ribbed leaves with reticulate venation. The roots of species of Smilax constitute Sarsaparilla.

The other sub-orders are: OPHIOPOGONOIDEÆ, of which Ophiopogon and Sansevieria are the more familiar genera: ALETROIDEÆ, Aletris (Star-Grass) cultivated in gardens: LUZURIAGOIDEÆ, Lapageria cultivated in greenhouses.

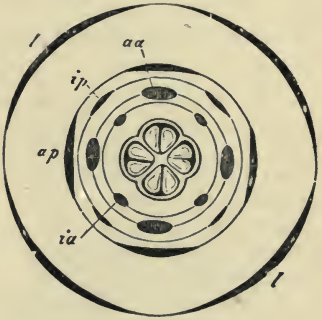

FIG. 364.—Diagram of the flower of *Paris quadrifolia*; *l* the foliage-leaves; *ap* the outer; *ip* the inner whorl of the perianth; *aa* outer; *ia* inner whorl of stamens. (After Sachs.)

Order 2. JUNCACEÆ. Floral formula, $K3$, $C3$, $A3+3$, $G_{(\bar{3})}$. Plants of a grass-like aspect; they differ from the preceding order in the dry and glumaceous character of the perianth, and in the starchy endosperm. The leaves are linear or tubular; the inflorescence is an anthela (see p. 493).

The species of Luzula, which has a unilocular three-seeded ovary, *multiflora*, *pilosa*, *campestris*, and *sylvatica*, are common in woods and on heaths. *Juncus* has a trilocular many-seeded ovary; plants of this genus are called Rushes; *J. glaucus* and *effusus* have a tubular stem and leaves, and a terminal inflorescence which is displaced laterally by a tubular bract which appears to be a prolongation of the stem; they are common in wet fields; *J. bufonius*, by waysides.

Order 3. PONTEDERIACEÆ. Water-plants of tropical America, with an irregular zygomorphic petaloid perianth: in other respects they resemble the Liliaceæ.

The commoner genera are Pontederia and Eichhornia: *Eichhornia azurea* and *crassipes* are frequently cultivated as hot-house aquatics.

SERIES II. EPIGYNÆ.

Ovary inferior.

Cohort 1. **Hydrales.** Order 1. HYDROCHARIDACEÆ. The inflorescence is at first enclosed in a spathe formed of a single bract, or more commonly of two connate bracts. The flowers have a perianth, the inner whorl being petaloid, and usually conform to the monocotyledonous type, but with pleiotaxy in the androecium and gynæceum; formula $K3$, $C3$, $A3 + 3 +$, $G_{\overline{(3 + \ldots)}}$. The flowers are usually monosporangiate and dioecious; the ♀ flowers have staminodia; the ♂ flowers have no gynæceum but an increased number of whorls in the androecium. Seeds generally numerous; without endosperm. Water-plants.

Fam. 1. *Hydrilleæ.* Ovary unilocular. Stem elongated, with whorls of small leaves.

Elodea (*Anacharis*) *canadensis* came originally from North America and has spread in our waters so as even to impede navigation in canals.

Fam. 2. *Vallisnerieæ.* Ovary unilocular. Stem short, with crowded leaves.

Vallisneria spiralis inhabits the lakes and ditches of the warmer parts of Europe. The leaves are long, narrow, and linear. The ♀ flowers are raised above water on long peduncles; the ♂ inflorescences break away from their peduncles and float about on the water to fertilise the ♀ flowers; the fruit ripens under water.

Fam. 3. *Halophileæ.* Perianth of outer whorl only; ovary unilocular.

Submerged marine plants, forming the single genus Halophila.

Fam. 4. *Stratioteæ.* Ovary 6- (or more) chambered. Stem short, with crowded leaves.

Stratiotes aloides (Water-Soldier) has stiff narrow leaves. *Hydrocharis Morsus Ranæ* is the Frog's Bit; the plant is small and floats on the water, with small roundly-cordate leaves.

Cohort 2. **Dioscoreales.** Flowers regular: floral formula $K3$, $C3$, $A3 + 3$, $G_{\overline{(3)}}$: fruit a berry or a capsule: endosperm oily.

Order 1. DIOSCOREACEÆ. The ovary is trilocular, with one or two ovules in each loculus: the flowers are monosporangiate and dioecious. They are climbing plants, with twining stems, having large above- or under-ground tubers, and usually triangular leaves with reticulate venation.

Dioscorea sativa, *Batatas* and others, known as Yams, are largely cultivated in the tropics, their tuberous roots yielding a food rich in starch. *Tamus communis*, the Black Bryony, is common in England.

Order 2. TACCACEÆ. The ovary is unilocular and many-seeded.

The flowers are ☿. They are tropical herbs, and the leaves which spring from the subterranean rhizome have reticulate venation.

Order 3. Bromeliaceæ. $K3$, $C3$, $A3 + 3$, $G\,(3)$. The ovary is superior, inferior, or semi-inferior, trilocular, with many seeds. Perianth heterochlamydeous. The leaves are usually long and narrow, sharply serrate; the stem is generally very short. The flowers are ☿, and form spikes or panicles with bracts.

Ananas sativa is the Pine-apple. The fruit is a berry, and the berries of each inflorescence coalesce into a spurious fruit (sorosis), above which the axis of the inflorescence extends and bears a crown of leaves (Fig. 365; see p. 528). In a state of cultivation the berries contain no seeds. It is a native of America, and is cultivated in all warm countries and in hot-houses.

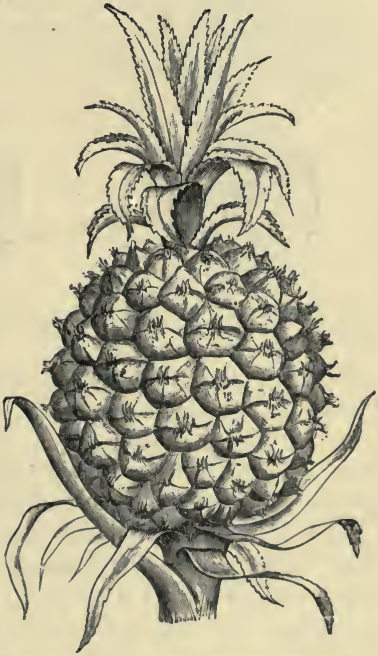

Fig. 365.—Fruit of the Pine-apple (reduced).

Cohort 3. **Amomales** (Scitamineæ). The flowers are irregular, zygomorphic or asymmetrical: general formula, $\downarrow K3,\ C3,\ A3+3,\ G_{\overline{(3)}}$, occasionally with a great reduction in the andrœcium. Perianth wholly petaloid, or the calyx may be sepaloid: ovary usually trilocular. Fruit, a capsule or a berry. Usually no endosperm, but abundant perisperm. They are tall herbaceous plants; the leaves are large and have pinnate venation.

Order 1. Musaceæ. $\downarrow K3,\ C3,\ A3+2\dagger 1$ or $0,\ G^{\underline{(3)}}$. Flower dorsiventral; the anterior external member of the petaloid perianth is usually very large, and the posterior always very small. In the family Museæ the odd sepal is anterior; the sepals are usually free, as are also the petals in Ravenala; but in Strelitzia the two lateral petals are connate, and in Musa the five anterior members of the perianth are connate, forming a tube which is open posteriorly: the posterior stamen is sterile or absent, and the others are not always fertile. The flower of the family Heliconieæ differs from this type in that the odd sepal is posterior, and the abortive posterior stamen belongs to the outer whorl. Seeds, one (Heliconia), or many, in each loculus, without endosperm. They are all shrubs of colossal growth, with enormously long leaves: the flowers are usually arranged in spicate inflorescences in the axils of large and often coloured bracts; sometimes several flowers spring from the axil of one bract.

Musa paradisiaca (Plantain), *M. Sapientum* (Banana), and *M. Ensete* are natives of the tropics of the Old World; the two former are now distributed throughout America and applied to a great variety of purposes; the fruit, which is of the nature of a berry, is an article of food, and the vascular bundles are used for making textile fabrics. The other genera are Ravenala, Strelitzia Heliconia.

FIG. 366.—Diagram of flower of Musa.

FIG. 367.—Diagrams of the two types of flower in the Zingiberaceæ. *A* Hedychium. *B* Alpinia.

Order 2. ZINGIBERACEÆ. ↓ $K3$, $C3$, A † 2 or 0+1 † 2, $G_{\overline{(3)}}$. Flower dorsiventral: calyx sometimes petaloid. Of the inner whorl of stamens the posterior alone bears a perfect anther, the other two being transformed into a usually petaloid body, the *labellum*. The outer whorl of stamens is absent, or but slightly indicated, in the Zingibereæ (Fig. 367 *B*); but is represented in the Hedychieæ and Globbeæ by two postero-lateral petaloid staminodes (Fig. 367 *A*). There is a small amount of endosperm in the seed, in a depression in the perisperm.

The commoner genera are Curcuma, Hedychium; Zingiber, Alpinia; Globba, having a unilocular ovary with three parietal placentæ.

The starch which is prepared from the rhizome of *Curcuma angustifolia* and *leucorrhiza* is known in commerce as East Indian arrowroot: Turmeric is obtained from the rhizome of *C. longa*. Cardamoms are the fruits of *Eletteria Cardamomum*. The dried rhizomes of *Zingiber officinale* are the common ginger.

Order 3. MARANTACEÆ or CANNACEÆ. $K3$, $C3$, $A0$ + 1 † 1, 0, or A † 2, 0+1 † 2, $G_{\overline{(3)}}$. Flower asymmetric: calyx not petaloid. The andrœcium is represented by a number of petaloid bodies, of which one only, the posterior stamen of the inner whorl, bears a bilocular anther (Fig. 368 *st*, *an*); of the staminodia one is larger than the others, and is reflexed, forming a *labellum* (Fig. 368 *l*); the narrow ones vary in number in the different species (Fig. 368 α and β): seed without endosperm; seeds numerous in Canna, single in each loculus in the other genera.

Canna indica and other species are commonly grown as ornamental plants.

Amylum Marantæ, the starchy meal prepared from the rhizome of *Maranta arundinacea*, is true or West Indian arrowroot.

Cohort 4. **Orchidales.** Flower irregular, dorsiventral, zygomorphic, gynandrous (see pp. 495, 518), reduced in the andrœcium: perianth petaloid. Seeds very small, without endosperm or perisperm; the embryo a minute undifferentiated mass of cells.

FIG. 368.—Flower of *Canna indica* (nat. size): *f* inferior ovary; *pa* the outer; *pi* the inner whorl of the perianth; *g* style; *st* the fertile stamen, with (*an*) the anther; *l* labellum; α and β the two staminodia. (After Eichler.)

Order 1. ORCHIDACEÆ. The flowers of most of the genera have the formula $\downarrow K3, C3, A1 + \dagger\ 2, G_{\overline{(3)}}$: those of the Cypripediinæ, however, have the formula $\downarrow K3, C3, A\ \dagger\ 1+2, G_{\overline{(3)}}$ (Fig. 369 *A*, *B*). The flower is generally so placed, in consequence of torsion of the ovary, that the posterior side of the flower, instead of being uppermost, as is normally the case, comes to lie inferiorly (*resupinate*), but there are exceptions (*e.g.* Liparis, Nigritella, Epipogium). The posterior segment (petal) of the inner whorl called the *labellum* (Fig 370, see also Fig. 294 *l*), is always larger than the others, and varies greatly in form; it frequently has a spur (Fig. 370 *sp*) or a sac-shaped cavity (Fig. 294). The andrœcium and the three stigmata are, in most Orchids, borne on a prolongation of the floral axis the *gynostemium* (Fig. 294 *s*; Fig. 372 *B* and *C gs*). In the andrœcium usually three stamens are represented: in the monandrous Orchids there is a fertile anterior stamen belonging to the outer whorl (Fig. 369, *A*), and often two staminodes, which are sometimes petaloid (*e.g.* Diuris) or small tooth-like prominences (auriculæ, stelidia) on the gynostemium (*e.g.* Orchis, Epipactis, Fig. 294 x), belonging generally to the inner andrœcial whorl, but sometimes apparently to the outer: in the diandrous Orchids (*e.g.* Cypripedium, Fig. 369 *B*) there are, generally, two fertile stamens belonging to the inner whorl; the outer whorl being only represented by an anterior staminode. The anther usually has four pollen-sacs, but may have two (*e.g.* Collabium) or eight (*e.g.* Calanthe, Bletia). In some genera the pollen-grains are separate from each other, in the majority they are united into a mass, *pollinium*, which fills an entire pollen-sac (Fig. 294 *E*, *F*, *p*). The pollinium may consist of tetrads with a common exine (*e.g.* Neottia); or of larger groups of cells, termed *massulæ* (*e.g.* Orchis), when it is said to be *sectile*; or of uniform tissue. In those Orchids which have pollinia, it is frequently the case that the tissue of the pollen-sac is prolonged, according to the position of the anther, either to the lower (*basitonous*, *e.g.* Ophrydinæ) or to the upper end of the anther (*acrotonous*, *e.g.* Phajiinæ, Oncidiinæ), and here almost exclusively gives rise to a mucilaginous filament, the *caudicle*, attached to the pollinium (or to the two or more pollinia of each half of the anther) below or above.

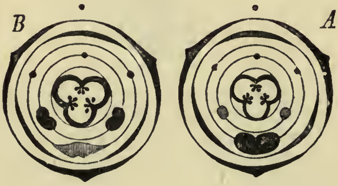

Fig. 369.—Diagram of Orchidaceous flowers, neglecting resupination. *A* The usual type. *B* Cypripedium: the shaded stamens are staminodia.

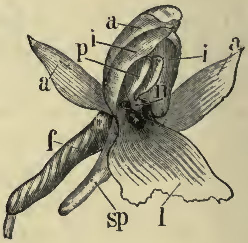

Fig. 370.—Flower of *Orchis mascula* (×2): *f* the twisted ovary; *a a a* the three outer perianth-leaves; *i i* two of the inner, *l* the third inner perianth-leaf, the labellum, with (*sp*) the spur; *n* stigma: *p* pollen-sacs.

The ovary is unilocular (rarely trilocular as in some Cypripediinæ), and contains numerous anatropous ovules on three parietal placentæ. In all the monandrous Orchids, the anterior lobe of the trilobate stigma is not susceptible of pollination, and is either rudimentary or developes into an organ termed the *rostellum* (Fig. 294 *h*), which is situated either above or below the anther, and in the tissue of which one or two small masses of sticky mucilage (*retinacula*) are formed, and are frequently enclosed in one or two pouches (*bursiculæ*) formed by the rest of the tissue of the rostellum. The pollinia adhere to the retinacula by the caudicle, when present, and are removed, in pollination, by the adhesion of the retinacula to the proboscis of the insect (see p. 456).

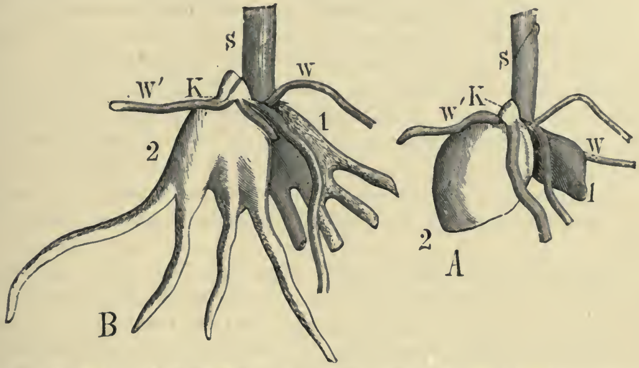

FIG. 371.—Tubers (*A*) of *Orchis Morio*; *B* of *Gymnadenia Conopsea*: *s* the peduncle; 1 this year's tuber; 2 next year's tuber; *k* the bud; *w* and *w′* roots (nat. size).

Most of the indigenous species have underground rhizomes or tubers. In the latter case, two tubers are usually present, the older one, which, at the time of flowering, becomes flaccid (Fig. 371 *A* and *B*, 1), throws up the flowering scape (*s*) or, in young plants, a short underground stem which produces only leaves above ground. At the upper end of this tuber another much firmer tuber is formed (Fig. 371), bearing at its apex the bud of the next year's stem (*K*). The tuber is to be regarded as a lateral bud which coalesces with its first root (or more than one, Fig. 371 *B*) and then increases in bulk: the lower end of an undivided tuber, as well as the ends of palmate tubers, has, in the young state at least, the same structure as the apex of a true root.

FIG. 372.—Flower of *Cypripedium Calceolus*: *p p* the leaves of the perianth have been cut away. *A* Side view. *B* Back view. *C* Front view; *f* ovary; *gs* gynostemium; *a a* the two fertile stamens; *s* staminode; *n* stigma. (After Sachs.)

The genera of Orchidaceæ are so numerous and so diverse that it is impossible to give more than a summary of those which are British.

DIANDRÆ: two fertile stamens, belonging to the inner whorl: all three lobes of the stigma are susceptible of pollination: pollen-grains cohering but slightly.

Fam. 1. *Cypripediinæ*. *Cypripedium Calceolus*, the Lady's Slipper, now very rare, occurs in woods in the north of England: it has a creeping rhizome and broad ovate leaves: the perianth is of a reddish-brown colour, except the labellum which is yellow and forms a shoe-like sac (Figs. 369, 372).

MONANDRÆ: one fertile stamen, the anterior, belonging to the outer whorl: only the two lateral lobes of the stigma are susceptible of pollination; the anterior lobe is rudimentary, or is developed as the rostellum: pollen-grains coherent into pollinia.

Fam. 2. *Ophrydinæ*: anther short and broad; the waxy pollinia are basitonous; a rostellum, forming retinacula to which the caudicles of the pollinia adhere.

To the sub-family *Serapiadeæ*, which is characterised by the short gynostemium and the erect anther, belong the genera Ophrys, Orchis, and Aceras. In Ophrys there are two distinct bursiculæ and retinacula, and the pollinia remain distinct: the flowers resemble insects: *O. apifera* the Bee Orchis, *O. aranifera* the Spider Orchis, and *O. muscifera* the Fly Orchis, occur in chalk pastures. In Orchis there is but one bursicula, but there are two retinacula, so the pollinia may be removed separately, and the labellum is spurred: *Orchis Morio*, *mascula*, and *militaris*, have round or oval tubers; whilst *O. latifolia*, *maculata*, and *pyramidalis* have palmate tubers. In Aceras (*Aceras anthropophora* is the green Man-Orchis) the 3-lobed lip is not spurred, and there is but one retinaculum.

To the sub-family *Gymnadenieæ*, characterised by the absence of a bursicula, and consequently bare retinacula, belong the British genera Gymnadenia, Habenaria, Neotinea, Herminium (as also other interesting European genera, such as Chamæorchis and Nigritella). In Gymnadenia (*G. Conopsea*, the fragrant Orchis) the retinacula are contiguous: in Habenaria (*H. albida*, *bifolia*, *viridis*, Butterfly Orchis) the retinacula are distant: in Neotinea (*N. intacta*) the pink perianth-segments are connivent: whilst in the preceding genera the labellum is spurred, it is not spurred in Herminium (*H. Monorchis*, the green Musk Orchis).

Fam. 3. *Neottiinæ*: pollinia usually soft and granular, either acrotonous or altogether without caudicles.

To the sub-family *Cephalanthereæ*, in which the labellum is transversely segmented, belong the genera Cephalanthera, Epipactis, and Epipogium. Cephalanthera (*C. grandiflora*, *C. ensifolia*, *C. rubra*) and Epipactis (*E. latifolia* and *E. palustris*), the Helleborines, are rhizomatous leafy plants with well-developed leaves on the peduncles: the labellum is not spurred, and the rostellum is rudimentary. *Epipogium Gmelini* is a saprophyte, has no roots, and its leaves are scaly and not green; it has granular pollinia with acrotonous caudicles, a rostellum producing a retinaculum, and a spurred labellum; the flower is not resupinate.

To the sub-family *Spirantheæ*, characterised by a rostellum as long as the anther, producing a retinaculum to which the granular pollinia (without caudicles) adhere, belong the genera Spiranthes, Listera, and Neottia. Spiranthes, Lady's Tresses (*S. autumnalis*, *æstivalis*, and *gemmipara*) has a spike unilateral by torsion, perianth-segments connivent, no spur. Listera, Tway-blade (*L. cordata* and *ovata*), has only two foliage-leaves, and spreading perianth-segments, no spur. *Neottia Nidus-Avis*, the Bird's-nest Orchid, is a saprophyte, with scaly leaves which do not contain chlorophyll ; labellum not spurred.

To the sub-family *Physureæ*, characterised by the structure of the pollinium, which is sectile, belongs the genus Goodyera (*G. repens*) in which the labellum has no spur, and the pollinia have acrotonous caudicles ; the inflorescence is, like that of Spiranthes, a unilateral twisted spike ; the plant is rhizomatous.

Fam. 4. *Liparidinæ*: the anther produces four waxy pollinia without caudicles. *Liparis* (*Sturmia*) *Loeselii*, has only two foliage-leaves and a pseudobulb; the flower is not resupinate ; there are two retinacula, to each of which a pair of pollinia become attached. Malaxis (*M. paludosa*, Bog Orchis) has a short gynostemium and a single retinaculum; reproduced by pseudo-bulbs. Corallorhiza (*C. innata*, the spurless Coral-root) is a saprophytic plant, without roots or foliage-leaves.

There are many other families, including a large number of genera which are mainly tropical and commonly epiphytic with aerial roots (see p. 155). Many of these are cultivated in hot-houses such as Oncidium, Vanda, Dendrobium, Angræcum, etc. Vanilla is the dried fruit of *Vanilla planifolia*, a climbing species.

Though pollination is usually dependent upon the visits of insects (see p. 456), self-pollination is by no means uncommon. For instance, among British Orchids, *Ophrys apifera* and *Neotinea intacta* are probably always self-pollinated, and *Neottia Nidus-Avis*, *Epipactis ovalis* and *E. latifolia*, are frequently self-pollinated, simply by the falling of the pollen on to the stigma. *Cephalanthera rubra* is commonly pollinated whilst in the bud, by the germination of the pollen-grains, the pollen-tubes making their way to the stigma.

Cohort 5. **Narcissales.** Flowers regular or irregular: not less than three stamens in the andrœcium : perianth petaloid : seeds with oily endosperm.

Order 1. AMARYLLIDACEÆ. $K3$, $C3$, $A3+3$ or 12 to 18, $G_{(\overline{3})}$, The flower is occasionally zygomorphic and narrowly funnel-shaped : anthers usually introrse. The fruit is usually a trilocular loculicidal capsule, sometimes a berry.

The principal of the numerous genera are arranged in the following families :—

Fam. 1. *Amaryllidoideæ :* subterranean stem, bulbous : scape leafless, bearing a single terminal flower, or an umbellate inflorescence, invested by one or more bracts. Amongst the genera without a corona (see p. 515) are Amaryllis (*A. Belladonna*, the Belladonna Lily), Vallota (*V. purpurea*, the Scarborough Lily) with zygomorphic flowers; Zephyranthes, Sternbergia, Crinum, Galanthus (*G. nivalis*, the Snowdrop), and Leucojum (*L. vernum*, the Spring Snowflake ; *L. æstivum*, the Summer Snowflake) with actinomorphic flowers. Amongst the genera with a corona are the many species of Narcissus *N.* (*Corbularia*) *Bulbocodium*, the Hooped Petticoat Daffodil; *N.* (*Ajax*) *Pseudo-narcissus*, the common Daffodil; *N.* (*Queltia*) *Jonquilla*, the Jonquil, and *N. incomparabilis* the Star Daffodil; *N. poeticus*, the Poet's or Pheasant's Eye Narcissus; *N. Tazetta*, the Cluster Narcissus: also the genera Pancratium and Eucharis.

Fam. 2. *Agavoideæ:* stem not subterranean, short or elongated into a trunk. Here belong the genera Agave (incl. Bonapartea) and Fourcroya. *Agave americana*, commonly known as the false or American Aloe, is a native of Mexico but has been naturalised in Southern Europe. The short stem bears a rosette of large thick prickly leaves: when it has attained sufficient vigour—in Southern Europe in from 10 to 20 years—it throws up a scape 20–30 feet high, which branches and bears a large number of flowers in a pyramidal panicle.

Fam. 3. *Hypoxidoideæ*: subterranean stem a rhizome, bearing a terminal flowering-shoot. Alstrœmeria, the Peruvian Lily, has a leafy flowering-shoot and the habit of a Lily.

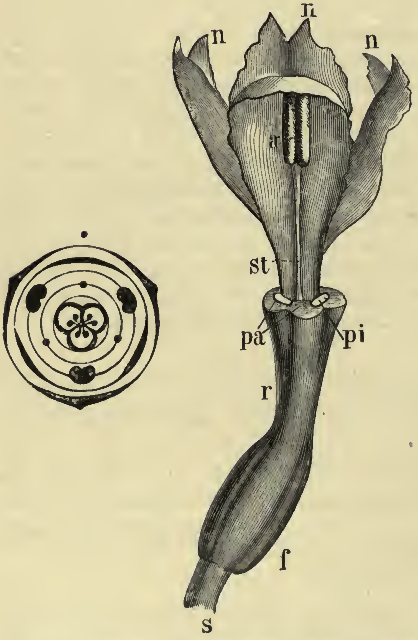

Fig. 373.—Diagram of the flower of Iris, and view of the same after the removal of the perianth: *s* peduncle; *f* inferior ovary; *r* tubular portion of the perianth; *pa* the insertion of the outer, *pi* of the inner leaves of the perianth; *st* stamen; *a* anther; *n n n* the three petaloid stigmata (nat. size).

The British species of the order are the common Daffodil, the Snowdrop, and the Snowflakes.

Order 2. IRIDACEÆ.

$K3$, $C3$, $A3+0$, $G_{\overline{(3)}}$. The flower is sometimes zygomorphic: stamens sometimes monadelphous; the anthers are extrorse: the fruit is usually a trilocular loculicidal capsule.

Fam. 1. CROCOIDEÆ: flowers actinomorphic, terminal, single, with sometimes other axillary flowers, each invested by a spathe: stem, a corm.

To this family belong, amongst others, the genera Crocus and Romulea. Many species of Crocus (*e.g. C. aureus, biflorus, speciosus, vernus*, etc.) are cultivated; *C. sativus* is the Saffron Crocus, the dried stigmata of which are termed Saffron: the only indigenous British species is *C. nudiflorus* which is autumn-flowering. *Romulea* (*Trichonema*) *Columnæ* occurs in the Channel Islands.

Fam. 2. IRIDIOIDEÆ: flowers mostly actinomorphic, forming many-flowered inflorescences of various form with spathes, each of which invests more than one flower: stem bulbous or rhizomatous.

This large family includes several sub-families, of which the following are the more important:—

Sub-fam. *Iridinæ:* perianth-tube short or absent; the capsule is not enclosed by the spathe; the styles are petaloid, with the stigma on the under surface. Iris, the Flag, is the principal genus. The species of this very large genus may be divided into two groups based upon the bulbous or the rhizomatous character of the stem. The most familiar of the bulbous Irises are, *I. xiphioides* (or *Xiphion latifolium*, or *Iris anglica*) the so-called English Iris; *I. Xiphium* (*Xiphion vulgare*) the Spanish Iris; *I. reticulata*, *persica*, and *Histrio.* The rhizomatous Irises are classified according to the presence or absence of hairs (beard) on the perianth-segments: thus,—

Sect. Hexapogon: all the perianth-segments bearded along the upper surface of the midrib of the claw: *e.g. I. longiscapa* and *falcifolia.*

Sect. Pogoniris: only the three outer perianth-segments bearded on the midrib of the claw; *e.g. I. florentina*, *germanica*, *pallida*, *pumila.*

Sect. Oncocyclus: the three outer perianth-segments bearded on both claw and limb: *e.g. I. susiana*, *iberica.*

Sect. Apogon: perianth-segments beardless: *e.g. I. graminea* and *siberica* with linear leaves; *I. Pseudacorus*, *ochroleuca*, *foetidissima*, etc., with ensiform leaves. *I. Pseudacorus* (Yellow Flag) and *foetidissima* are British.

Sub-fam. *Tigridinæ*: perianth-tube absent; styles branched with an apical stigma; the inner whorl of perianth-segments is smaller than the outer; stamens monadelphous: bulbous plants. *Tigridia Pavonia* is the Tiger Flower.

Sub-fam. *Sisyrinchinæ:* perianth-tube short; styles unbranched, nearly cylindrical, alternate with the stamens (not opposite as in Iris): stamens free, or connate at the base: rhizomatous plants.

Here belong the genera Libertia (with free stamens) and Sisyrinchium (with basally connate stamens), having actinomophic flowers; *S.* (*Bermudiana*) *angustifolium*, Blue-eyed Grass, occurs in Galway.

Sub-fam. *Aristinæ*: perianth-tube elongated; capsule enclosed by the spathe; stamens monadelphous (Patersonia) or free (Aristea); generally rhizomatous.

Fam. 3. IXIOIDEÆ: the flowers, which are frequently zygomorphic, are each invested by a spathe: stem, usually a corm.

In the sub-fam. *Ixieæ*, the zygomorphism of the flower is but slightly marked: Schizostylis is rhizomatous, whilst the other genera (Ixia, Geissorhiza, etc.) are bulbous.

In the *Gladioleæ*, the zygomorphism of the flower is well-marked, but the flower may be either straight and erect (*e.g.* Tritonia, Montbretia, Sparaxis), or curved (*e.g.* Gladiolus). *Gladiolus illyricus* (*communis*), the lesser Gladiolus or Corn-Flag occurs in England.

In the *Watsonieæ* (Watsonia, Lapeyrousia, Freesia), the styles are 2-branched.

Class X.—DICOTYLEDONES.

The ripe seed (Fig. 295) may be albuminous, containing a mass of endosperm and a relatively small embryo, as in the Umbelliferæ and Euphorbiaceæ ; but sometimes the embryo is relatively large and the endosperm occupies only a small space, as in the Labiatæ: more commonly the seed is exalbuminous, the endosperm being wholly absent, and then the embryo, which has large and fleshy cotyledons, fills the entire cavity of the testa, as in the Rosaceæ, the Leguminosæ, and the Compositæ. Perisperm is rarely present, either together with endosperm (*e.g.* some Piperales and Nymphæaceæ), or alone (Chenopodiales).

The embryo (see p. 443) usually has distinct members, consisting of an axis and two opposite cotyledons ; in rare cases, *e.g.* Corydalis, only one cotyledon is present, or abnormally three may occur, as is occasionally the case in the Oak, the Sycamore, and the Almond. In parasites and saprophytes which are devoid of chlorophyll and which have very small seeds, such as Monotropa and Orobanche, the embryo is quite undifferentiated, and it consists of only a small number of cells.

The axis of the embryo frequently persists as the main axis of the plant which grows in length and produces numerous less vigorous lateral shoots ; but it often happens that some of these lateral branches subsequently grow as vigorously as the main axis : when this is the case, and when also the lower and feebler shoots die off, a head, such as is common in forest-trees, is the result ; in the case of shrubs, vigorous branches are formed quite low down on the main stem. The branching of the stem is almost invariably axillary and lateral: it is frequently monopodial (p. 40), but in many forest-trees the stem (trunk) and branches form a sympodium, the uppermost lateral bud growing each year in the direction of the main axis, which does not itself develope any further.

When the axis of the embryo continues to be the main axis of the plant, the primary root also developes greatly, and forms a tap-root from which the lateral roots grow in acropetal succession ; in cases in which the growth in length of the tap-root is limited, numerous adventitious roots spring from its older portions ; these may again give rise to lateral roots, and by a repetition of this process an elaborate root-system is formed.

The stem is almost always monostelic (see p. 152). The vascular bundles of the stem are almost always conjoint, collateral, and open, and the stem grows in thickness by the activity of the cambium-ring which is formed (p.191).

The epiblema of the root is (except Nymphæaceæ) the persistent innermost layer of the original many-layered epidermis (see p. 154). When the stem grows in thickness, the root does so also (see p. 191).

The leaves exhibit infinite variety both in their relative position and in their form. The foliage-leaves almost always consist of petiole and blade; amplexicaul leaf-bases are comparatively rare, but stipules, on the contrary, are very common. Branching or segmentation of the leaves is common, and is frequently indicated by the incision of the margin. The usually reticulate venation of the leaves is characterized by the presence of a large number of veins which project on the under surface, except in thick, fleshy

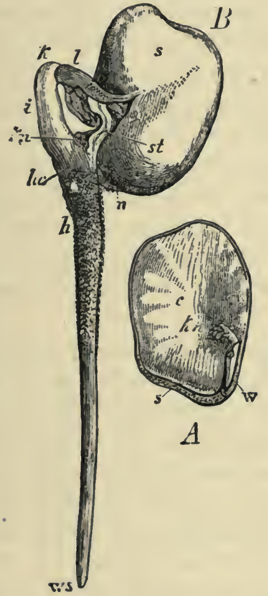

FIG. 374.—*Vicia Faba*, the Bean. *A* Seed with one of the cotyledons removed; *c* the remaining cotyledon; *w* radicle; *kn* plumule; *s* testa. *B* Germinating seed; *s* testa; *l* a portion of the testa torn away; *n* hilum; *st* petiole of one of the cotyledons; *k* curved epicotyl; *hc* the very short hypocotyl; *h* the primary root; *ws* its apex; *kn* bud in the axil of one of the cotyledons.

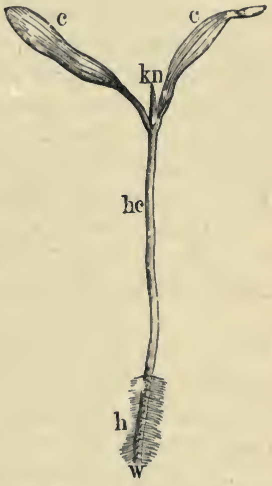

FIG. 375.—Seedling of the Maple (nat. size): *c c* the cotyledons; *kn* the plumule; *hc* the hypocotyl; *w* primary root; *h* root hairs (the lower part is cut off).

leaves, and which frequently anastomose; a midrib is almost always present, giving off lateral branches to right and left.

The flowers, when they are lateral, are usually furnished with two prophylla or bracteoles (see p. 505): they differ very considerably in their structure, and cannot be referred to any one type. The following are the principle forms:

1. In a considerable number the perianth, which is simple, and the andrœcium are isomerous, consisting of four, five, or six members; their arrangement is either spiral ($\frac{2}{5}$), or whorled so that the stamens are always superposed on the leaves of the perianth; the latter are all similar and are sepaloid. Formula $P5 \mid A5$, or $P\text{n} + \text{n}$, $A\text{n} + \text{n}$, where $\text{n} = 2$ or 3. This structure prevails in some of the Monochlamydeæ (Urticales, Amentales).

2. In a second group, all the parts of the flower are arranged in a continuous spiral, the stamens, and sometimes the carpels, being generally more numerous than the leaves of the perianth: the perianth may consist only of a calyx, or a corolla may be developed in place of the external stamens; when this is the case the corolla alternates with the calyx, provided that it is isomerous with it, as in most Ranales.

3. With these two types are connected by many intermediate forms those flowers in which the biseriate perianth and the stamens are in whorls: their formula is $K\text{n}$, $C\text{n}$, $A\text{n} + \text{n}$, where n usually $= 5$ or 4. This is the most common type of structure of the flower; it occurs in most Polypetalæ and Gamopetalæ; it may be modified either by the suppression of one (usually the inner) whorl of stamens, or by their multiplication, their branching, or their cohesion, or by the suppression of the corolla.

4. Finally, there remain certain flowers which cannot be directly referred to any one of the above types, and they must therefore be left unexplained for the present, and the relationships of their families must remain uncertain.

The sub-divisions in which the Dicotyledons are arranged in the following classification are especially characterized by peculiarities in the structure of the flower. It is impossible, however, to draw sharp distinctions between the sub-classes, the cohorts, the orders, and sometimes even between the families, for the position of a plant in the system depends, not upon any one character, but upon the aggregate of its characters.

The principal orders of Dicotyledons may be arranged as follows:—

SUB-CLASS I. MONOCHLAMYDEÆ.

Cohort I. **Piperales.**
- Order 1. PIPERACEÆ.
- ,, 2. CHLORANTHACEÆ.
- ,, 3. SAURURACEÆ.

Cohort II. **Urticales.**
- Order 1. URTICACEÆ.
- ,, 2. MORACEÆ.
- ,, 3. CANNABINACEÆ.
- ,, 4. ULMACEÆ.

Cohort III. **Amentales.**
- Order 1. BETULACEÆ.
- ,, 2. CORYLACEÆ.
- ,, 3. FAGACEÆ.
- ,, 4. JUGLANDACEÆ.
- ,, 5. MYRICACEÆ.
- ,, 6. CASUARINACEÆ.
- ,, 7. SALICACEÆ.

Cohort IV. **Proteales.**
- Order 1. PROTEACEÆ.

Cohort V. **Chenopodiales.**
- Order 1. CHENOPODIACEÆ.
- ,, 2. AMARANTACEÆ.
- ,, 3. PHYTOLACCACEÆ.
- ,, 4. NYCTAGINACEÆ.

Cohort VI. **Asarales.**
- Order 1. ARISTOLOCHIACEÆ.
- ,, 2. CYTINACEÆ.

Cohort VII. **Santalales.**
- Order 1. SANTALACEÆ.
- ,, 2. LORANTHACEÆ.
- ,, 3. BALANOPHORACEÆ.

SUB-CLASS II. POLYPETALÆ.

SERIES I. THALAMIFLORÆ.

Cohort I. **Ranales.**
- Order 1. RANUNCULACEÆ.
- ,, 2. MAGNOLIACEÆ.
- ,, 3. CALYCANTHACEÆ.
- ,, 4. NYMPHÆACEÆ.

Cohort II. **Menispermales.**
- Order 1. MENISPERMACEÆ.
- ,, 2. BERBERIDACEÆ.
- ,, 3. LAURACEÆ.
- ,, 4. MYRISTICACEÆ.
- ,, 5. POLYGONACEÆ.
- ,, 6. CERATOPHYLLACEÆ.

Cohort III. **Caryophyllales.**
- Order 1. CARYOPHYLLACEÆ.
- ,, 2. PORTULACEÆ.
- ,, 3. AIZOACEÆ.

Cohort IV. **Parietales.**
- Order 1. PAPAVERACEÆ.
- ,, 2. FUMARIACEÆ.
- ,, 3. CRUCIFERÆ.
- Order 4. CAPPARIDACEÆ.
- ,, 5. RESEDACEÆ.
- ,, 6. CISTACEÆ.
- ,, 7. BIXACEÆ.
- ,, 8. VIOLACEÆ.

Cohort V. **Sarraceniales.**
- ,, 1. SARRACENIACEÆ.
- ,, 2. NEPENTHACEÆ.
- ,, 3. DROSERACEÆ.

Cohort VI. **Guttiferales.**
- Order 1. HYPERICACEÆ.
- ,, 2. TAMARICACFÆ.
- ,, 3. ELATINACEÆ.
- ,, 4. TERNSTRŒMIACEÆ.
- ,, 5. CLUSIACEÆ.
- ,, 6. DIPTEROCARPACEÆ.

Cohort VII. **Malvales.**
- Order 1. TILIACEÆ.
- ,, 2. STERCULIACEÆ.
- ,, 3. MALVACEÆ.

SERIES II. DISCIFLORÆ.

Cohort I. **Geraniales.**
- Order 1. Geraniaceæ.
- „ 2. Linaceæ.
- „ 3. Erythroxylaceæ.
- „ 4. Oxalidaceæ.
- „ 5. Balsaminaceæ.
- „ 6. Tropæolaceæ.
- „ 7. Zygophyllaceæ.
- „ 8. Rutaceæ.
- „ 9. Meliaceæ.
- „ 10. Simarubaceæ.
- „ 11. Burseraceæ.

Cohort II. **Sapindales.**
- Order 1. Sapindaceæ.
- „ 2. Aceraceæ.
- „ 3. Polygalaceæ.
- „ 4. Anacardiaceæ.

Cohort III. **Celastrales.**
- Order 1. Celastraceæ.
- „ 2. Staphyleaceæ.
- „ 3. Aquifoliaceæ.
- „ 4. Thymeleaceæ.
- „ 5. Elæagnaceæ.
- „ 6. Rhamnaceæ.
- „ 7. Ampelidaceæ.

Cohort IV. **Euphorbiales.**
- Order 1. Euphorbiaceæ.
- „ 2. Buxaceæ.
- „ 3. Empetraceæ.
- „ 4. Callitrichaceæ.

SERIES III. CALYCIFLORÆ.

Cohort I. **Umbellales.**
- Order 1. Umbelliferæ.
- „ 2. Araliaceæ.
- „ 3. Cornaceæ.

Cohort II. **Passiflorales.**
- Order 1. Passifloraceæ.
- „ 2. Papayaceæ.
- „ 3. Begoniaceæ.
- „ 4. Cucurbitaceæ.
- „ 5. Cactaceæ.

Cohort III. **Myrtales.**
- Order 1. Onagraceæ.
- „ 2. Haloragidaceæ.
- „ 3. Lythraceæ.
- „ 4. Myrtaceæ.
- „ 5. Rhizophoraceæ.

Cohort IV. **Rosales.**
- Order 1. Rosaceæ.
- „ 2. Leguminosæ.
- „ 3. Platanaceæ.

Cohort V. **Saxifragales.**
- Order 1. Saxifragaceæ.
- „ 2. Crassulaceæ.
- „ 3. Cephalotaceæ.
- „ 4. Pittosporaceæ.
- „ 5. Hamamelidaceæ.
- „ 6. Podostemaceæ.

SUB-CLASS III. GAMOPETALÆ.

SERIES I. HYPOGYNÆ.

Cohort I. **Lamiales.**
Order 1. Labiatæ.
,, 2. Verbenaceæ.
,, 3. Globulariaceæ.
Cohort II. **Personales.**
Order 1. Scrophularaceæ.
,, 2. Plantaginaceæ.
,, 3. Bignoniaceæ.
,, 4. Acanthaceæ.
,, 5. Gesneraceæ.
,, 6. Orobanchaceæ.
,, 7. Lentibulariaceæ.
Cohort III. **Polemoniales.**
Order 1. Convolvulaceæ.
,, 2. Polemoniaceæ.
,, 3. Solanaçeæ.
,, 4. Boraginaceæ.
Cohort IV. **Gentianales.**
Order 1. Gentianaceæ.
,, 2. Loganiaceæ.
,, 3. Apocynaceæ.
,, 4. Asclepiadaceæ.
,, 5. Oleaceæ.
Cohort V. **Ebenales.**
Order 1. Sapotaceæ.
,, 2. Ebenaceæ.
,, 3. Styraceæ.
Cohort VI. **Primulales.**
Order 1. Primulaceæ.
,, 2. Myrsinaceæ.
,, 3. Plumbaginaceæ.
Cohort VII. **Ericales.**
Order 1. Ericaceæ.
,, 2. Epacridaceæ.
,, 3. Diapensiaceæ.
,, 4. Pyrolaceæ.
,, 5. Vacciniaceæ.

SERIES II. EPIGYNÆ.

Cohort I. **Campanales.**
Order 1. Campanulaceæ.
,, 2. Lobeliaceæ.
Cohort II. **Rubiales.**
Order 1. Rubiaceæ.
,, 2. Caprifoliaceæ.
Cohort III. **Asterales.**
Order 1. Valerianaceæ.
,, 2. Dipsaceæ.
,, 3. Compositæ.

SUB-CLASS I. MONOCHLAMYDEÆ.

The flowers have a simple, usually sepaloid, perianth, or it may be absent; they are commonly monosporangiate.

It must not be assumed that all Dicotyledons with apetalous flowers belong to this sub-class: on the contrary, many such plants must, in view of the aggregate of their characters, be placed in the other sub-classes. The plants included here are such as have flowers the perianth of which appears to be *primitively* simple, and not such as have flowers the perianth of which seems to have become simple by suppression (see p. 505).

Cohort I. **Piperales.** The flowers are usually ambisporangiate, and they are arranged in a spike or a spadix, with bracts; perianth usually absent. Ovary usually superior, monomerous or trimerous, unilocular. Ovule orthotropous, solitary, basal or suspended; in some cases there are several parietal ovules. The embryo is small and lies imbedded in endosperm, usually in a depression of the abundant perisperm (Fig. 295 *B*, p. 458).

Order 1. PIPERACEÆ. Ovary superior, usually trimerous or monomerous, unilocular, with a single orthotropous, erect, central ovule. The inflorescence is a long spadix, with usually peltate subtending bracts (Fig. 376 *f*, *below*), in the axils of which the flowers are situated. The flower consists only of a ovary (Fig. 376 *f*, *above*) and generally six, three, or sometimes two stamens; the fruit is a berry.

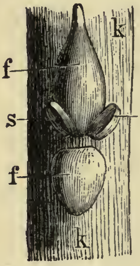

FIG. 376.—Part of the spadix of Peperomia, with a flower: *f* (below) the subtending bract; *s s* the two stamens; *f* (above) ovary; *k* surface of the spadix (mag.).

Piper nigrum is a climbing shrub belonging to the East Indies; the unripe dried fruits are black pepper; white pepper consists of the ripe fruits of the same plant, which, after maceration, are freed from their outer coat. Cubebs are the fruits of *Piper Cubeba* of Java.

Order 2. CHLORANTHACEÆ. Flowers sometimes with a rudimentary perianth. Ovary inferior, monomerous, with a single suspended ovule. Seed with oily endosperm, but no perisperm. Tropical or sub-tropical.

Order 3. SAURURACEÆ. Flowers without perianth. Gynæceum of three or four carpels, either apocarpous or syncarpous: in the former case each ovary bears 2–4 orthotropous ovules on its ventral suture (marginal placentation); in the latter case the unilocular ovary bears 6–10 ovules on each parietal placenta; ovary superior. Seed as in Piperaceæ. Herbs with a rhizome, belonging to North America and Eastern Asia.

Houttuynia cordata (see p. 48) is a common weed in Japan and China.

Cohort II. **Urticales.** Flowers usually diclinous, in inflorescences of various forms: perianth usually present, simple. sepaloid, consisting typically of five ($\frac{2}{5}$) or reduced to four $(2+2)$ segments; stamens equal in number and opposite to the segments of the perianth, in consequence, apparently, of the essentially spiral arrangement of the floral organs (see p. 497); ovary superior, monomerous, unilocular, or sometimes dimerous, with two styles, and then rarely bilocular: ovule solitary, in different positions. Seed commonly containing endosperm. The inflorescences in orders 1–3 are usually situated two together at the base of a leafy dwarf-shoot which springs from the axil of a leaf, and they are cymose (Fig. 377). The leaves are generally hirsute. Cystoliths (p. 108) are commonly present.

Fig. 377.—Part of the stem of *Urtica urens*, with a leaf (*f*) in the axil of which is the branch (*m*), at the base of which are the inflorescences (*b*), without any bracts (nat. size).

Order 1. Urticaceæ. Ovary monomerous: ovule central, orthotropous, erect. Seed containing endosperm. They are mostly herbs or shrubs without milky juice and frequently provided with stinging-hairs: leaves alternate, stipulate. Flowers polygamous, monœcious, or diœcious, in paniculate or glomerulate inflorescences.

Urtica urens and *dioica* (Stinging Nettles) are known by the stinging hairs which are distributed over their whole surface: perianth 2 + 2; the two outer segments of the perianth of the ♀ flower are larger than the inner segments (Fig. 378 *B*). In the former species the ♂ and ♀ flowers are contained in the same panicle, and the floral axis is but feebly developed; in the latter they are on different plants, and the axis is well developed and bears leaves. *Böhmeria nivea*, a native of China and Japan, has strong bast-fibres used for weaving the material known in England as Grass-cloth. *Parietaria officinalis*, Wall-Pellitory, having polygamous flowers with a gamophyllous perianth, and destitute of stinging-hairs, occurs occasionally on walls, by roadsides, etc.

Order 2. Moraceæ. Ovary generally dimerous, and sometimes bilocular (Artocarpus): ovule suspended, anatropous or campylotropous, more rarely basal and orthotropous: seed with or without endosperm; the fruit is enveloped by the perianth (usually 2 + 2), which becomes fleshy, or by a fleshy floral axis. Trees and shrubs with milky juice, scattered leaves and caducous stipules.

Fig. 378.—*A* staminal ♂; *B* carpellary ♀ flowers of the Stinging Nettle, Urtica: *p* perianth; *a* stamen; *n′* rudimentary ovary of the ♂ flower; *ap* outer; *ip* inner whorl of the perianth; *n* stigma of the ♀ flower (mag).

Morus alba and *nigra* (Mulberry) come from Asia; the flowers are disposed in short catkins; the catkins are borne singly on shoots, which, at the time of flowering, are still buds, and they contain monosporangiate, but monœcious, flowers; the ♀ flowers give rise, as ripening takes place, to a spurious fruit (sorosis, p. 528), consisting of spurious drupes formed by the perianths. The leaves, particularly of the former species, are the food of the silkworm. *Broussonetia papyrifera* (Paper Mulberry) has flowers like the preceding, but they are diœcious: the bark is made into paper in China and Japan. *Maclura tinctoria*, in Central America, yields Fustic, a dye. *Ficus Carica* is the Fig-tree of Southern Europe; the fig itself (termed a syconus) is the deeply concave axis of the inflorescence, on the inner surface of which the flowers and subsequently the fruits, in the form of hard grains (achenes), are borne (Fig. 379 *mf*); the cavity is closed above by small bracts (Fig. 379 *b*). *Ficus elastica* is the India-rubber tree; it is frequently cultivated in rooms. *F. religiosa* and other East Indian species yield Caoutchouc, which is their inspissated milky juice (latex). *Ficus indica* is the Banyan. *Artocarpus incisa* is the Bread-fruit tree of the South Sea Islands; the large spurious fruit (sorosis) of this tree is roasted and eaten as bread. *Galactodendron utile*, the Cow-tree of Columbia, has a nutritious latex, while that of *Antiaris toxicaria* (Java) is poisonous.

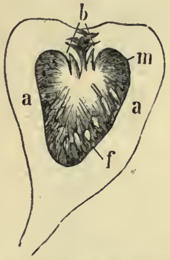

FIG. 379.—Longitudinal section of a Fig (nat. size): *a a* fleshy axis of the inflorescence; *f* ♀, *m* ♂, flowers; *b* bracts.

Order 3. CANNABINACEÆ. Ovary dimerous, unilocular: ovule suspended, campylotropous: seed with endosperm. Flowers diœcious: the ♂ flowers (Fig. 380 *A*) have a 5-partite perianth and 5 short stamens; the ♀ flowers have a tubular entire perianth (Fig. 380 *B*, *p*) enclosed in a bract (Fig. 380 *B*, *d*). Herbs with decussate leaves—at least the lower ones—and persistent stipules; devoid of latex.

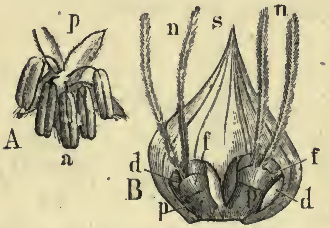

FIG. 380.—*A* ♂ flower of the Hop: *p* the perianth; *a* stamens. *B* Part of ♀ inflorescence: *p* perianth; *f* ovary, with two stigmata (*n*); each flower is enclosed in its bracteole (*d*); *s* scale, *i.e.* one of the two stipules, from the common axil of which the branch bearing the flowers springs.

Cannabis sativa, the Hemp, a native of Asia, is cultivated throughout Europe. The ♂ inflorescences are panicled dichasia or scorpioid cymes, and are disposed on both sides of a rudimentary shoot at the apex of the plant; the ♀ flowers are placed singly on both sides of a similar shoot, which bears secondary shoots in the axils of its leaves, each having two flowers. The tough bast-fibres are used in weaving and for ropes; the seeds contain a great deal of oil. *Humulus Lupulus*, the Hop, is both cultivated and found wild. The stem, which has the peculiarity of twining to the right, bears its leaves in pairs; each leaf has a pair of membranous stipules. In the inflorescence the leaves (bracts) are placed singly, and are finally represented only by their stipules. In the ♀ inflorescence, which somewhat resembles a fir-cone, a rudimentary shoot is present in the common axil of each pair of stipules, and bears two flowers on each side; it seems at first sight as if two flowers were developed in the axil of each stipule (Fig. 380 *B*). All the scales and bracts are covered, especially on the upper surface, with numerous yellow glands. In the ♂ inflorescence the shoot which bears the flowers is well developed.

Order 4. ULMACEÆ. Ovary dimerous, sometimes bilocular, but generally unilocular by abortion. Ovule suspended and solitary. Flowers mostly ambisporangiate, with a 4–6-partite perianth (Fig. 381 *A*). Woody plants devoid of milky juice: leaves alternate, with caducous stipules. The inflorescences (glomerules) are borne directly in the axils of the leaves.

In the genus Ulmus the compact dichasial inflorescences are developed in the axils of the leaves (either persistent or deciduous), of the previous year, and they are invested by bud-scales; one or more flowers are developed in the axil of each of the more internal scales (bracts), and they open before the unfolding of the leaves. The ovary is sometimes bilocular. The fruit is a samara, that is, an achene with a broad membranous wing (Fig. 381 *B*). The leaves are alternate, and always oblique. The annual shoots have no terminal bud, and so they form a sympodium. Two species of Elm are indigenous in England. *Ulmus campestris*, the common Elm, and *Ulmus montana*, the broad-leaved Wych, or Scotch, or Mountain Elm: the former has rather slender branches, leaves with distinct petioles and crenate serrate margins, somewhat narrow at the base, and a seed which is above the centre of the samara; the latter has thick horizontally-spreading branches, leaves with very short petioles and doubly serrate margins, broad at the base, and a seed which is central in the samara. *Celtis australis*, from Southern Europe and *C. occidentalis*, from North America, are often cultivated as ornamental trees; their flowers are polygamous, and are placed singly or several together in the axils of the oblique accuminate leaves: the fruit is drupaceous.

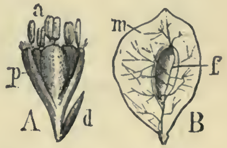

FIG. 381.—*A* Flower of *Ulmus montana* (mag.): *d* bract; *p* perianth; *a* stamens. *B* Fruit (samara) (nat. size): *m* membranous margin (wing).

Cohort III. **Amentales.** The flowers, which are always diclinous and generally monœcious, are arranged in catkins (amenta). The perianth, when it is present, consists typically of 5 ($\frac{2}{5}$) segments; or it may deviate from the type so as to consist of four, (*i.e.* 2 + 2), or six (*i.e.* 3 + 3) segments: the stamens, when their position can be determined, are superposed on the segments of the perianth for the reason given in the case of the Urticales (see p. 576).

The ovary is either superior or inferior, di- or tri-merous, with few ovules. The fruit (with the exception of Order 7, the Salicaceæ) becomes by abortion one-seeded, and is indehiscent: the seed has no endosperm. The flowers are furnished with bracts which often form investments for the fruit: their arrangement in most of the orders is as follows; in the axil of a scaly bract (the bracts being arranged spirally in the amentum) is a flower (*b*) with two bracteoles *α* and *β*, in the axil of each of which is another flower with two more bracteoles *α′* and *β′* (Fig. 382). The plants are trees and shrubs.

Order 1. BETULACEÆ. The flowers are monœcious, but in different catkins. The ♀ flowers have no perianth: the ovary is bilocular, with two ovules: the fruit is one-seeded, indehiscent, without any investment: the bract is coherent with the two or four bracteoles (the bracteoles *α′* are always absent) to form a three- or five-lobed scale, which does not adhere to the fruit.

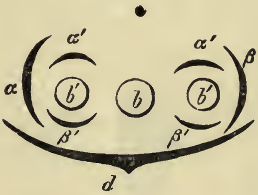

FIG. 382.—Typical diagram of a group of flowers in the Amentales: *d* bract; *b* the median flower with its bracteoles, *α* and *β*; *b′b″* the two lateral flowers, with their bracteoles *α′* and *β′*.

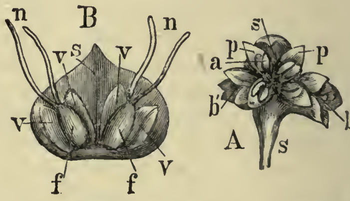

FIG. 383.—*A* Scale from a ♂ catkin of *Alnus incana*: the axillary branch adheres to the scale (*s*), it bears four bracteoles and three flowers: two of the flowers are seen laterally (*b′ b′*), the median one from above; *p* perianth; *a* stamens. *B* Bract (*s*) of a ♀ catkin of the same plant: its axillary branch bears two lateral branches, each of which bears two bracteoles (*v v*) and one flower; *f* the ovary; *n* the stigmata (magnified and diagrammatic).

Alnus, the Alder. In the ♂ amenta three flowers with four bracteoles (*α*, *β*, *β′*, *β′*) occur in the axil of the bract, each flower having a perianth of four segments, and four unbranched stamens. In the ♀ amenta the median flower is absent; the four bracteoles coalesce with the primary bract (Fig. 383 *B*, *v s*) to form a five-lobed woody scale which persists after the fall of the fruit which is not winged. The ♂ catkins are borne terminally, and the ♀ laterally on the highest lateral branch, on the shoots of the previous year; they are not enclosed by bud-scales during the winter, and blossoming takes place before the unfolding of the leaves. The leaves have usually a ⅓ arrangement: in *A. incana*, the White Alder, the leaves are acuminate and gray on the under surface; in *A. glutinosa*, the black or common Alder, they are obovate or even emarginate, and green on both surfaces. In *Alnus viridis*, the mountain Alder, only the ♂ catkins are destitute of bud-scales in the winter: the fruit is winged.

Betula, the Birch. In both kinds of catkins the three flowers have only the bracteoles α and β. In the ♂ flowers the perianth is usually incomplete, and there are only two stamens, the filaments of which are forked. In the ♀ catkins, the two bracteoles cohere with the bract to form a three-lobed scale which falls off together with the winged fruit. The ♂ catkins are borne terminally on the shoots of the previous year, and are not covered with bud-scales during the winter; the ♀ catkins are borne terminally on lateral dwarf-shoots which have only a few leaves, and they are enclosed by bud-scales during the winter; as a consequence, flowering takes place after the unfolding of the leaves. The shoots of successive years form sympodia, and the leaves are arranged spirally. *B. verrucosa* has white glands on the leaves and young shoots: *B. pubescens* has no glands, but the shoots are hairy; it is a northern form: *B. fruticosa* and *B. nana* are shrubs occurring in high latitudes: *B. alba* is the common Birch.

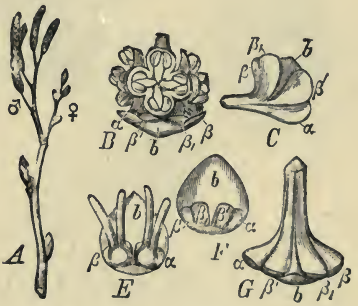

FIG. 381.—*Alnus glutinosa.* *A* Branch bearing catkins (in winter). *B* a group of ♂ flowers (from above). *C* The same after removal of flowers (lateral view). *E* Group of ♀ flowers, seen from within. *F* The same after the removal of the flowers. *G* a scale from the ♀ catkin: *b* bract; α, β, β' bracteoles.

Order 2. CORYLACEÆ. Flowers monœcious, in ♂ and ♀ catkins. The ♂ flowers have no perianth; that of the ♀ flower is rudimentary. The inferior ovary is bilocular; one loculus is sterile, the other contains two suspended anatropous ovules: the fruit is one-seeded and indehiscent (a nut). Two flowers are borne in the axil of the bract of the ♀ catkin, the median flower being absent. The one-seeded fruit is surrounded by a leafy investment (cupule) formed by the three bracteoles ($\alpha\ \alpha_{,}\ \beta_{,}$ and $\beta\ \alpha_{,}\ \beta_{,}$ respectively, Fig. 382) of each side. In the ♂ catkin the median flower only is developed: the filaments of the stamens are deeply forked.

In Corylus, the Hazel, the ♀ catkin resembles a bud, since the external sterile bracts have the same structure as the bud-scales (Fig. 385 *B*); the red stigmata project at the top; the investment of the fruit is irregularly cut; a small projection is formed on the fruit, the nut, by the remains of the epigynous perianth. Each bract of the ♂ amentum bears two bracteoles α and β, and a flower consisting of four forked stamens (Figs. 385–6). Both kinds of amenta are placed in the axils of the leaves of the previous year, and are not enclosed by scales during the winter; hence flowering takes place before the unfolding of the leaves. Leaves distichous. *C. Avellana* is the common Hazel; a variety of *C. tubulosa*, with red leaves, the Purple or Blood Hazel, is cultivated as an ornamental shrub.

In Carpinus, the Hornbeam, the fruit has a three-lobed cupule (Fig. 387), the fruit is ribbed and is surmounted by the perianth. The bract of the ♂ catkin bears 4–10 deeply forked stamens; there are no bracteoles. The catkins of both kinds are borne at the apex of short leafy shoots of the same year, hence flowering takes place after the unfolding of the leaves. Leaves distichous. The annual shoots form sympodia. *C. Betulus* has an irregular stem and serrate leaves which are plicate along the lateral veins. In Ostrya (Southern Europe) the investment of the fruit is an open tube.

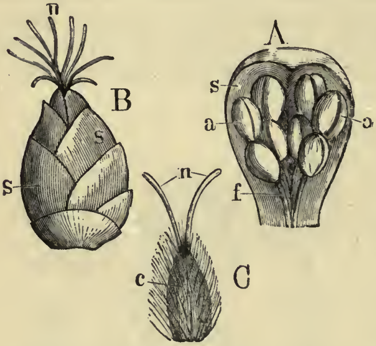

FIG. 385.—*Corylus Avellana.* *A* Bract (*s*) of a ♂ catkin, with a ♂ flower: stamens (*f*), and anthers (*a*). *B* ♀ catkin: the lower bracts (*s*) have no flowers: the stigmata (*n*) project above. *C* A single ♀ flower surrounded by the cupule (bracteoles) (*c*), with two stigmata (*n*) (mag. and diag.)

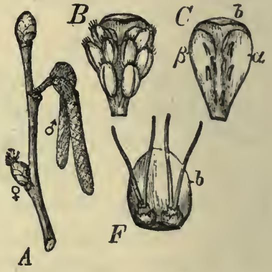

FIG. 386.—*Corylus Avellana.* *A* Flowering branch. *B* ♂ flower with its bract. *C* Bract after the removal of the anthers. *F* Group of ♀ flowers seen from within: *b* bract.

Order 3. FAGACEÆ. Flowers monœcious, with a perianth of five or six segments. Ovary inferior, trilocular, with two ovules in each loculus; ovules anatropous, ascending or suspended; the fruit is one-seeded and indehiscent (a nut); it is invested by a cupule formed probably by the connate bracteoles $\alpha' \beta' \alpha' \beta'$ (Fig. 382), and having its surface covered with scales, prickles, etc. The filaments are not forked.

In Quercus, the Oak, the ♂ catkins are loose; each bract bears a single flower in its axil without bracteoles: the perianth is 5–7 lobed, and the stamens from 5–10 or indefinite (Fig. 388 *A*). There is a single flower, the median one, in the axil of each bract of the ♀ catkin; thus the cupule invests only a single fruit, and forms the so-called cup at its base. The leaves are developed in $\frac{2}{5}$ order, and are aggregated towards the apices of the annual shoots; the annual shoots are always terminal. The ♂ catkins are borne in the axils of the uppermost bud-scales (pairs of stipules) on both long and dwarf-shoots of the same year; the ♀ catkins in the axils of the foliage-leaves of the terminal shoots: flowering takes place shortly after the unfolding of the leaves. The ovules are ascending. The hypogean cotyledons remain enclosed in the testa during germination. *Quercus Robur* is the English species, of which there are two varieties, *Quercus pedunculata* and *Quercus sessiliflora*: the former has elongated ♀ catkins, so that the fruits are widely separated from each other, and its pinnately lobed leaves are shortly stalked and cordate at the base: the latter has compact ♀ catkins, so that the fruits form a cluster, and its leaves have longer petioles, and are narrowed at the base. *Quercus Suber* is the Cork-Oak of Southern Europe. There are also several North American species.

In Fagus, the Beech, the catkins of both kinds are stalked dichasial clusters, borne each in the axil of a foliage-leaf. The flowers have no bracts, or bracteoles, except the cupule of the ♀ flower. The flowers of the pendulous ♂ catkin are closely packed; they have a perianth of 4–7 segments, and 8–12 stamens. The erect ♀ catkin consists of two flowers only, which are invested by a tetramerous cupule. The cupule is covered with hard bristles, and when ripe splits into four valves to allow the two triquetrous fruits to escape; each fruit bears at its apex a brush-like remnant of the perianth. The ovules are suspended. The ♀ inflorescences are borne on erect axes in the axils of the leaves of the apical shoot of the same year, the ♂ on pendulous axes springing from the axils of the lower leaves of the shoot. Leaves distichous, approaching each other on the under surfaces of the shoots, their axillary buds approaching each other on the upper surface: the winter buds are elongated and pointed. The epigean cotyledons escape from the seed on germination. *Fagus sylvatica* is the common Beech: varieties with tinted leaves, such as the Purple Beech and the Copper Beech, are commonly cultivated.

FIG. 387. – Fruit of *Carpinus Betulus* with three-lobed cupule.

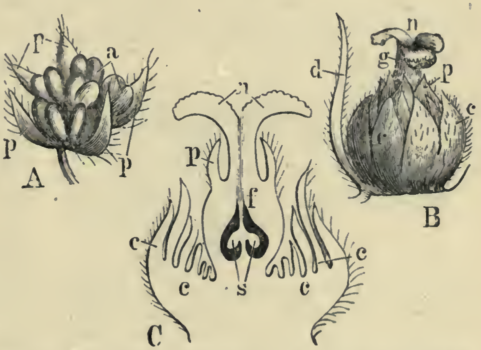

FIG. 388.—*Quercus pedunculata.* *A* ♂ flower magnified *p* perianth; *a* stamens. *B* ♀ flower magnified: *d* bract; *c* cupule; *p* the epigynous perianth; *g* the style; *n* the stigma. *C* The same, still more magnified, in longitudinal section; *f* ovary; *s* ovules.

In Castanea, the edible or Spanish Chestnut, some of the catkins consist at their lower part of ♀ flowers and at their upper of ♂ flowers, whilst others have only ♂ flowers. In the axil of each bract there are usually either seven ♂ or three ♀ flowers: the latter are invested by the bracteoles α and β, and by a cupule formed by the other four bracteoles; the cupule, which is covered with prickles, completely encloses the fruit until it is ripe, when it splits into four valves. Both kinds of catkins are formed in the axils of leaves of shoots of the same year, the mixed catkins being nearer to the apex than the ♂ ones, The ovules are suspended. The leaves are arranged spirally on vigorous shoots; they are distichous on the less vigorous lateral shoots. *C. vulgaris*, from Southern Europe, is cultivated in parks; it has undivided toothed leaves.

Order 4. JUGLANDACEÆ. Flowers monœcious, the two kinds of flowers being contained in distinct catkins. Each bract bears in its axil a single flower with two bracteoles. The ♀ flower has usually a perianth: the inferior ovary is dimerous, and encloses a single erect orthotropous ovule. The ♂ flowers are usually borne on the bract; they may or may not have a perianth, and the stamens are indefinite (Fig. 389 *A*). The fruit is drupaceous; the leaves are pinnate, and, like the flowers, they are aromatic.

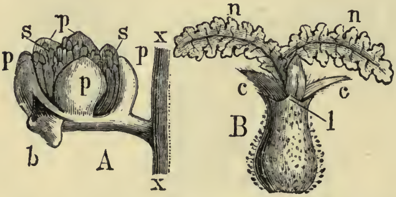

FIG. 389.—*A* Bract of the ♂ catkin of *Juglans nigra* bearing a flower: *p* perianth and bracteoles; *s* stamens; *x* axis of the catkin. *B* ♀ flower of the same plant: *l* bracteoles; *c* perianth; *n* stigmata (magnified).

In Juglans the ♂ catkins are borne on the apices of the leafless shoots of the previous year, and the few-flowered ♀ catkins on the apices of the leafy shoots of the same year. The bracteoles of the ♀ flowers (Fig. 389 *l*) grow up around the ovary. The succulent mesocarp is thin, and ruptures irregularly; the hard endocarp opens on germination along the line of junction of the two carpels, and then the incurved margins of the carpels are seen as an incomplete longitudinal septum projecting between the two cotyledons of the embryo which is closely invested by the endocarp. *J. regia*, the Walnut Tree, is a native of Southern Europe: in North America, *J. cinerea* and *nigra* occur; also various species of Carya, the Hickory, remarkable for its very hard wood.

Order 5. MYRICACEÆ. Trees or shrubs; the flowers, which are diclinous and sometimes diœcious, are arranged in catkins; perianth absent. The ovary is dimerous and unilocular, with one erect orthotropous ovule.

Myrica Gale, the Bog-Myrtle, is a shrub occurring on moors. *M. cerifera*, belonging to North America, secretes a quantity of wax on its drupaceous fruits.

Order 6. CASUARINACEÆ. Trees having somewhat the appearance of Horse-tails (Equisetum), with long channelled internodes, and leaves forming a toothed sheath. The monœcious flowers are in distinct catkins; the ♂ flowers consist of a single axial stamen (see p. 78) and two perianth-leaves: the ♀ of a dimerous unilocular ovary invested by two bracteoles, which, when ripe, are hard and woody; the whole ♀ catkin then resembles a pine-cone: ovules, generally two, orthotropus, ascending. (For peculiarities of fertilisation, etc., see p. 528.)

Several species of Casuarina are indigenous in Australia.

Order 7. SALICACEÆ. The diœcious flowers are arranged in amenta, and they are borne in the axils of the bracts without any bracteoles. There is no perianth, but each flower contains a glandular disc or nectary. The ovary is dimerous and unilocular, and contains a number of parietal ovules. The dehiscence of the fruit is loculicidal; the numerous seeds are furnished with a pencil of silky hairs at their bases (p. 459). The catkins are developed at the ends of lateral dwarf-shoots which always bear scales or even a few foliage-leaves.

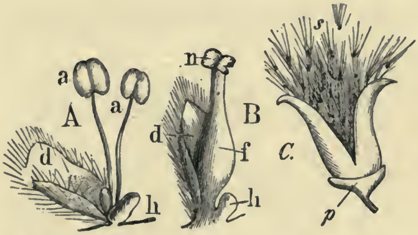

FIG. 390.—*A* ♂, *B* ♀ flower of Salix: *d* bract; *h* disc; *a* stamens; *f* ovary; *n* stigmata (enlarged). *C* Dehiscent fruit of the Poplar: *s* seeds; *p* disc.

Salix, the Willow or Sallow, has entire bracts, a one or two-toothed nectary in each flower, and usually two stamens, entire shortly-stalked leaves, and its winter-buds are covered by a scale which is formed by the coalescence of two. The shoots, which grow throughout the summer, die down yearly. Some species, such as *S. alba*, *fragilis*, and *babylonica*, the Weeping Willow, have pendulous branches, and are arborescent: most of them are shrubby, and some, such as *S. reticulata*, *retusa*, and *herbacea* are small decumbent shrubs occurring in the Alps and in high latitudes. In *S. purpurea* and *incana* the two stamens are connate: *S. triandra* has three stamens. Most of the species grow on the banks of rivers; *S. aurita* and *caprea* in forests, and *S. repens* and others on moors.

Populus, the Poplar, has toothed or lobed bracts, a cup-shaped nectary (Fig. 390 *C*, *p*), and numerous (4–30) stamens; the leaves are often lobed and have long petioles; the winter-buds are enclosed by a number of scales; the shoots have a terminal bud. In the Section Leuce the young shoots are pubescent, and the buds are not viscid; the ♂ flowers have usually only from 4–8 stamens, and the stigmata have 2–4 lobes: to this section belong *P. alba*, the White

Poplar or Abele, with five-lobed leaves on the elongated shoots, which are white and woolly beneath; and *P. Tremula*, the Aspen, with sinuate-serrate leaves, glabrous beneath, which are versatile on the long slender and compressed petiole, and which are therefore very readily set in motion by the wind. In the Section Aigeiros, the young shoots and the buds are viscid and glabrous; the bracts are glabrous, and the number of stamens is usually from 15–30; the stigmata are entire or shortly lobed: to this section belong *P. nigra*, the Black Poplar, and a variety with erect branches, the Lombardy Poplar; of the latter, only ♂ individuals are usually cultivated. In the Section Tacamahaca, the young shoots and buds are viscid; the leaves grey below, with compressed petioles; and the stamens 20–30: to this section belongs *P. balsamifera* of North America and Siberia.

Cohort IV. **Proteales.** Characters, those of the natural order.

Order 1. PROTEACEÆ. Affinities doubtful. Flowers ambisporangiate; the very short stamens are superposed on the four segments of the simple perianth, and are adnate to them (Fig. 391 *B*): when the flower opens, the tube of the perianth often becomes still more deeply cleft: the superior monomerous ovary is usually borne upon a prolongation of the axis (Fig. 391 *C*, *gp*): ovules one or more, ascending: seeds without endosperm.

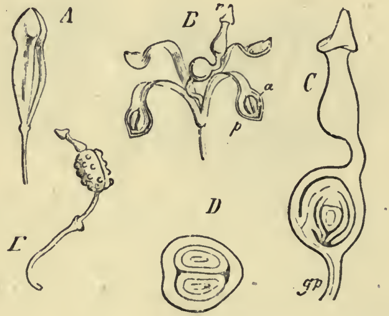

FIG. 391.—Flower of *Manglesia glabrata*. *A* Before opening. *B* Open: *p* segment of the perianth; *a* anther; *n* stigma. *C* Ovary (below) in longitudinal section; *gp* gynophore. *D* Transverse section of the ovary. *E* Ripe fruit. (After Sachs.)

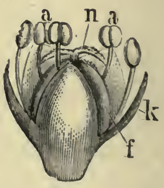

FIG. 392.—Flower of Chenopodium (enlarged): *k* perianth; *a* stamens; *f* ovary; *n* stigma.

Protea, Grevillea, Manglesia, and others occur mostly in South Africa and in Australia.

Cohort V. **Chenopodiales.** Flowers usually ambisporangiate; perianth sepaloid or petaloid: ovary monomerous or polymerous; ovule usually solitary; embryo coiled or curved: ripe seed contains perisperm, but no endosperm.

This cohort is sometimes placed, though apparently without sufficient reason, in the sub-class Thalamifloræ close to the Caryophyllaceæ, with which order it is, however, connected by the Phytolaccaceæ.

Order 1. CHENOPODIACEÆ. Flowers small, united to form a dense inflorescence: the bracteoles are frequently suppressed. Stamens typically equal in number to and superposed on the usually four (2 + 2) or five ($\frac{2}{5}$) free or connate sepaloid perianth-leaves for the same reason as in the Urticales (p. 576) (Fig. 392). Ovary usually medially dimerous and unilocular, with a single campylotropous, erect or horizontal, basal ovule. Stipules wanting.

Chenopodium album, the Goose-foot, and *C. Bonus Henricus*, the All-good, are common weeds on garden-ground and waste land. *Spinacia oleracea* is Spinach, cultivated as a vegetable. *Beta vulgaris* is cultivated under the var. *Cicla* (Mangold); *B. altissima* is the species used in the manufacture of sugar, and *B. rubra* is the red Beetroot; *B. maritima* is the wild Beet. Salsola, the Salt-wort, and its allies, Suæda, the Sea-blite, and Salicornia, the Marsh-Samphire or Glass-wort, with fleshy stems and leaves, are conspicuous in the vegetation of the sea-shore. Atriplex, the Orache, is the other British genus.

Order 2. AMARANTACEÆ. The flowers have the same structure as those of the preceding family: they usually have bracteoles which are frequently petaloid: perianth sometimes petaloid: ovary unilocular, apparently di- or tri-merous: ovule solitary and basal, but in some cases (Celosia) the ovules are numerous. Stipules absent. The flowers usually form dense inflorescences.

Species of Amaranthus and Celosia (Cock's-comb), the latter having a monstrous floral axis, are well known as ornamental plants. *Amaranthus Blitum* is found wild in Britain.

Order 3. PHYTOLACCACEÆ. The flowers have a simple, generally 5-leaved, perianth which is often petaloid, and there are frequently two regularly alternating whorls of stamens; when there is but one whorl of stamens they are sometimes superposed on the perianth-leaves (Microtea); the number of the stamens in one or both whorls is in many cases doubled (Fig. 393): the number of carpels varies very much; when the ovary is polymerous it is multilocular, each loculus containing a single ascending ovule. Stipules occasionally present.

FIG. 393.—Diagram of the flower of *Phytolacca decandra*.

The juice of the berries of *Phytolacca decandra*, a native of North America, is used as a colouring-matter in the manufacture of wine and in other processes.

Order 4. NYCTAGINACEÆ. Perianth a simple whorl, petaloid, gamophyllous, 5-leaved; the basal portion persists as an investment to the fruit, often becoming succulent or woody: stamens in greater or smaller numbers (1–30); when isomerous they usually alternate with the perianth-leaves, but are sometimes opposite to them (Colignonia): ovary monomerous, unilocular, with one basal campylotropous ovule; the flowers are surrounded by an involucre or epicalyx of 3, 5, or many bracts, enclosing 1, 3, or many flowers.

Mirabilis Jalapa, the Marvel of Peru, is an ornamental plant from America; the roots are often substituted for those of the true Jalap. Whilst generally sepaloid, the involucre is petaloid in Bougainvillea where it encloses three flowers, and in Tricycla where it encloses but one: in the latter case, as the single flower appears to be terminal, the involucre may be more correctly described as an epicalyx of bracteoles (see p. 494). The embryo of Abronia is pseudo-monocotyledonous.

Cohort VI. **Asarales.** Affinities doubtful. Flowers mono- or ambi-sporangiate: ovary inferior: ovules numerous.

Order 1. ARISTOLOCHIACEÆ. Flowers 3–6-merous, ambisporangiate: perianth of three connate petaloid segments forming a three-lobed tube: stamens 6 or 12, with extrorse anthers: ovary usually 6-locular, with numerous ovules in two longitudinal rows along the inner angles of each loculus. The minute embryo is enclosed in the copious endosperm. They are herbs or shrubs, often climbing, with large leaves.

In *Asarum europæum* (Asarabacca) the three lobes of the perianth are equal; alternating with them are three scales which probably represent a corolla: the twelve stamens (apparently in two whorls) are free, and the connective is produced (Fig. 394). The annual shoots of the creeping stem bear four cataphyllary leaves, two large petiolate reniform foliage-leaves, and a terminal flower. The lateral branches spring from the axils of the uppermost foliage-leaf and of the scales. In Aristolochia, the Birthwort (see Fig. 293, p. 456), the limb of the perianth is obliquely lipped; the six anthers are sessile and adnate to the short style (see p. 518). *A. Sipho* is a climber frequently cultivated: *A. Clematitis*, though not indigenous, is found wild in Britain, generally on ruins: the

FIG. 394.—*Asarum europæum.* Longitudinal section of the flower (mag.); *p* perianth. (After Sachs.)

flowers of the latter occur usually several together in the axils of the leaves, and those of the former in pairs, one above the other, together with a branch, in the axils of the leaves of the shoot of the previous year.

The presence in Asarum of what is apparently a corolla renders the position of this order among the Monochlamydeæ rather doubtful.

Order 2. CYTINACEÆ. Parasites devoid of chlorophyll and without foliage-leaves, with a usually deformed vegetative body, and either solitary flowers of remarkable size, or small flowers in a compact inflorescence. Flowers of various structure, mono- or ambi-sporangiate: perianth campanulate: the stigmata and anthers are borne on a central column: ovary generally unilocular: ovules very numerous, having generally one or two integuments: embryo rudimentary: seed with or without endosperm.

Sub-order 1. CYTINEÆ. Flowers monosporangiate. *Cytinus Hypocistis* is parasitic on the roots of Cistus in Southern Europe; another species occurs in Mexico, and another in South Africa.

Sub-order 2. HYDNOREÆ. Flowers ambisporangiate. Hydnora is parasitic on the roots of Euphorbiæ, etc., in South Africa; Prosopanche is parasitic on the roots of Prosopis in South America: the seed contains both endosperm and perisperm.

Sub-order 3. RAFFLESIEÆ. Rafflesia and Brugmansia are parasitic on the roots of Ampelidaceæ and Leguminosæ in the Malay Archipelago: Pilostyles belongs to tropical South America. *Rafflesia Arnoldi* is conspicuous for the enormous size of its flower. Brugmansia has ambisporangiate flowers.

Cohort VII. **Santalales.** Parasitic plants: leaves, when present, entire: stamens equal in number to the leaves of the perianth and superposed upon them: ovary inferior, unilocular; ovules usually devoid of integument.

Order 1. SANTALACEÆ. Parasites provided with chlorophyll: flowers generally ambisporangiate: ovules 1–4, suspended, upon a free central placenta: perianth 3–5-lobed; fruit a nut or drupe: seed with endosperm.

Thesium linophyllum, the Bastard Toad-flax, is an indigenous plant which is parasitic on the roots of other plants. The leaves are narrow and linear. The bracts of the flowers, which are disposed in racemes, are usually placed high up on the pedicels, close under the flowers, and in most of the species constitute with the bracteoles a three-leaved epicalyx. The stamens are filiform, inserted at the base of the lobes of the perianth. The perianth is persistent, remaining curled up at the apex of the indehiscent fruit (Fig. 395 *B*). *Santalum album*, an East Indian tree, yields Sandal-wood.

Order 2. LORANTHACEÆ. Parasites provided with chlorophyll: flowers mono- or ambi-sporangiate; sometimes diœcious: perianth of 4, 6, or 8 leaves: ovary 1–2-merous: in the free central placenta, which becomes more or less closely adherent to the wall of the ovary, are developed several embryo-sacs, each of which probably represents an ovule, but usually one only is fertile: fruit a berry: seed generally with endosperm.

Viscum album, the Mistletoe, is parasitic on various trees, forming conspicuous evergreen bunches. The stem bears a pair of opposite leaves (Fig. 396 *b b*), from the axils of which new branches spring, each bearing a pair of cataphyllary leaves and then a pair of foliage-leaves, while the main axis ceases to grow, or produces a terminal inflorescence, consisting of three flowers (Fig. 396 *h f*): branches or inflorescences may also spring from the axils of the cataphyllary leaves. The flowers are diœcious. The fruit is a one-seeded berry with a viscid pericarp, by means of which the seeds become attached to trees, and thus effect the distribution of the plant. The ♂ flowers have multilocular sessile anthers which are inserted (Fig. 396 *B a*) upon the leaves of the perianth. *Loranthus europæus* occurs upon Oaks in Eastern Europe.

FIG. 395.—*A* Flower; *B* fruit of *Thesium montanum*: *f* ovary; *p* perianth; *s* stamens; *n* stigma (enlarged).

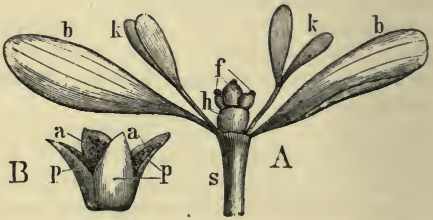

FIG. 393.—*A* Terminal shoot of a ♀ plant of the Mistletoe, *Viscum album*: *s* stem; *b b* leaves; *k k* axillary buds; *f* three ♀ flowers with the fruit set; *h* bracts. *B* ♂ flower (mag.) *p* perianth; *a* anthers adherent to the leaves of the perianth.

Order. 3. BALANOPHORACEÆ. Parasites devoid of chlorophyll and without foliage-leaves, with a deformed vegetative body. Flowers diœcious or monœcious, in many-flowered inflorescences. The staminate flowers have usually a 3–4-lobed perianth. The carpellary flowers have usually no perianth, and consist of a one-seeded ovary of 1–3 carpels: the ovule is suspended, and it frequently adheres closely to the ovary; an integument is present in Cynomorium. The embryo is very small.

Balanophora, Lophophytum, and others are Brazilian genera; others (Mystropetalon, Sarcophyte) inhabit tropical Africa; *Cynomorium coccineum* is found in the Mediterranean region.

SUB-CLASS II. POLYPETALÆ.

Flowers usually ambisporangiate : perianth usually consisting of calyx and corolla, the petals being free.

SERIES I. THALAMIFLORÆ.

Sepals usually free : petals often indefinite : stamens hypogynous, often indefinite : gynæceum apocarpous or syncarpous.

Cohort I. **Ranales.** Flowers generally acyclic or hemicyclic : perianth consisting of calyx only, or of calyx and corolla : stamens usually indefinite : gynæceum apocarpous, sometimes reduced to a single carpel; very rarely syncarpous, with a multilocular ovary. Seed with or without endosperm.

Order 1. RANUNCULACEÆ. Perianth either consisting of a petaloid calyx, or of calyx and corolla, usually spiral : stamens numerous, occupying several turns of the spiral, or arranged in several alternating whorls; anthers usually with lateral dehiscence, sometimes extrorse or introrse : carpels numerous, spirally arranged; rarely one only; the ovules are disposed on the connate margins of each carpel, that is, in two rows down the ventral suture; in several genera the number of the ovules in each ovary is reduced to one, which then originates from either the upper or the lower end of the cavity of the ovary : seed with endosperm. They are almost all herbaceous plants, and are either annuals or they have perennial rhizomes; they have no stipules, but they have amplexicaul leaves.

Tribe 1. *Anemoneæ.* Petals generally replaced by stamens : sepals frequently petaloid : ovaries numerous, each containing a single suspended or ascending anatropous ovule ; fruit consists of a number of achenes.

The genus Clematis consists of shrubs which creep, or climb by their petioles, and have opposite leaves, and a petaloid usually valvate calyx. *Clematis Vitalba*, the Old Man's Beard, is common in hedges; it has a greenish-white calyx, and fruits with long feathery styles ; *C. Viticella*, *patens*, and others are cultivated as decorative plants. *Atragene alpina*, occurring in the Alps and in Siberia, has its external stamens converted into petaloid staminodes.

Thalictrum; the species of this genus, as *T. majus*, *minus*, *flavum*, and *alpinum*, the Meadow-Rues, have stems well covered with leaves, and flowers with an inconspicuous, fugacious, 4–5-leaved calyx, and a flat receptacle.

Anemone has an hemispherical receptacle (Fig. 397 *A t*), and a petaloid, usually 5–6-leaved calyx. In most of the species the underground rhizome elongates into an erect scape which bears a single whorl of three bracteoles forming an epicalyx (p. 494), beneath the terminal flower. In *A. nemorosa*, *ranunculoides*, and others, these bracteoles resemble the foliage-leaves, and often bear flowers in their axils; but in *A. Pulsatilla*, and others, they differ from the foliage-leaves in that they are palmatifid (Fig. 397 *A h*); in *A. Hepatica*, in which the scapes spring from the axils of cataphyllary leaves, the three bracteoles are simple and lie so closely under the petaloid calyx that at first they appear to be the calyx of the flower.

Myosurus minimus (Mouse-tail) has a very long cylindrical receptacle, bearing the indefinite spirally arranged carpels: stamens 4–14; the 5 sepals are spurred. Adonis, the Pheasant's Eye, has completely acyclic flowers; sepals 5, petals 8 or more, not glandular at the base; stamens and carpels indefinite, arranged in $\frac{5}{13}$ order: *A. autumnalis* is the species which occurs in England.

In Ranunculus, the calyx, which is not petaloid, consists of 5 ($\frac{2}{5}$) sepals, and the corolla of 5 imbricate petals which alternate with the sepals and have a nectary at their base: the stamens and carpels are arranged spirally; anthers extrorse; the ovule is ascending, whereas it is suspended in all the preceding genera. The genus includes water-plants with finely-divided leaves and white flowers, as *R. aquatilis*, Water Crowfoot, *fluitans*, etc.; and land- or bog-plants, usually with a yellow corolla, as *R. acris*, the Buttercup, *repens*, *bulbosus*, and *sceleratus* (all known as Crowfoot), and *Lingua* and *Flammula* (the Greater and

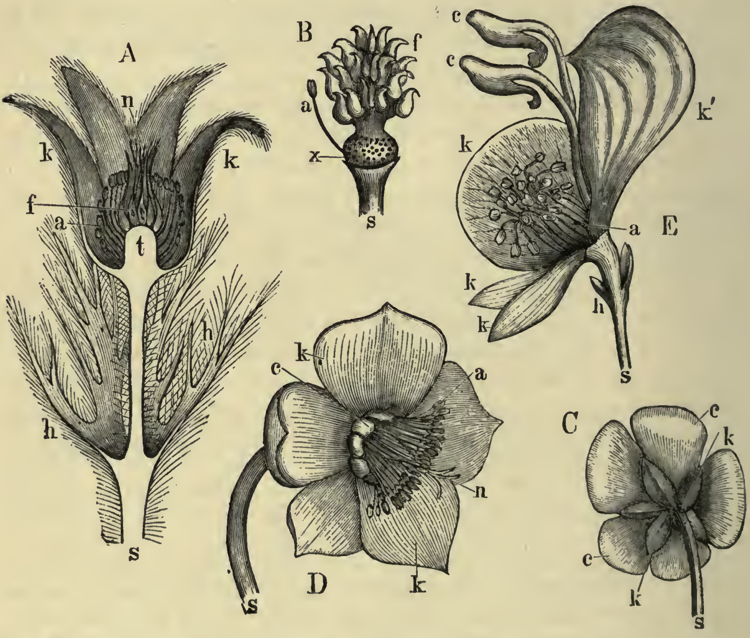

FIG. 397.—Flowers of Ranunculaceæ: *s* peduncle; *k* sepals; *c* petals; *a* stamens; *f* ovary; *n* stigma (all of natural size or slightly magnified). *A* Flower of *Anemone Pulsatilla* in longitudinal section; *h* epicalyx; *t* receptacle. *B* Gynæceum of Ranunculus: *x* receptacle with the points of insertion of the stamens which have been removed: *C* flower seen from below. *D* Flower of *Helleborus viridis*. *E* Flower of *Aconitum Napellus*: *h* bracteoles; *k′* hooded posterior sepal—the lateral sepal on this side is removed.

Lesser Spearworts); they are all more or less poisonous. *R. Ficaria* (the Lesser Celandine) has 3 sepals and usually 8 petals.

Tribe 2. *Helleboreæ.* Perianth generally consisting of calyx and corolla, the latter being occasionally suppressed; the petals are glandular at the base: ovaries usually fewer in number than the leaves of the perianth; ovules numerous, borne on the ventral suture; fruit usually consists of several follicles.

(*a*) With regular, generally actinomorphic, flowers:

Helleborus, with acyclic flowers; sepals more or less petaloid in $\frac{2}{5}$ arrangement; the petals, which are small and tubular, in $\frac{3}{8}$ or $\frac{5}{13}$; stamens in $\frac{5}{31}$ or $\frac{8}{21}$; ovaries usually 3–5 (Fig. 397 *D*). *H. niger* is the Christmas Rose; *H. viridis* and *fœtidus* are not rare. Nigella has 5 petaloid sepals and usually 8 (superposed if 5) small glandular petals: its carpels cohere partially or completely, forming a septicidal capsule. Trollius, the Globe-flower, has 5–15 petaloid sepals, and a similar number of small petals which, like the stamens and carpels, are all arranged spirally: *T. europæus* occurs in sub-alpine regions. Caltha, the Marsh-Marigold, has 5 yellow petaloid sepals, but no corolla: *C. palustris* is common in damp places. Eranthis, the Winter Aconite, has a 3-leaved epicalyx, and small petals with long claws. Actæa has a petaloid calyx and an alternating (sometimes suppressed) corolla; it has a single carpel which becomes a baccate fruit: *A. spicata*, the Baneberry or Herb Christopher, occurs in woods. Aquilegia, the Columbine, has a cyclic flower (Fig. 398): it has 5 petaloid sepals, and petals with long spurs; there are several whorls of stamens: *A. vulgaris*, *atrata*, *Aklei*, and others occur wild, or are cultivated as decorative plants.

FIG. 398.—Diagram of flower of Aquilegia.

(*b*) With irregular dorsiventral flowers:

Delphinium, the Larkspur, has the posterior of the 5 petaloid sepals prolonged into a spur: there are typically 5–8 petals, of which only the 2 (*D. Ajacis*; see Fig. 328 *A*) or 4 (*D. Staphisagria*) posterior are developed; the spurs of the two posterior petals project into that of the posterior sepal: *D. Staphisagria* has 3–5 carpels; *D. Consolida* and *D. Ajacis*, common garden plants, have usually but one carpel. In Aconitum, the Wolf's-bane or Monk's-hood, the posterior of the 5 petaloid sepals is large and hooded; the two posterior of the 8 petals have long claws, and are covered by the posterior sepal, the others being inconspicuous (Fig. 397 *E*, *c*).

Tribe 3. *Pæonieæ.* The perianth consists of calyx and corolla, and the petals are not glandular: ovaries with numerous ovules, surrounded by a disc: fruit of several follicles.

In Pæonia, the Peony, the flower is acyclic: the calyx consists of 5 sepals which gradually pass into the foliage-leaves; the petals are 5 or more. *P. officinalis*, *corallina*, and others are cultivated as decorative plants; *P. Moutan* has a woody stem and a tubular disc.

Order 2. MAGNOLIACEÆ. Perianth cyclic, consisting usually of three alternating trimerous whorls, one of sepals and two of petals: stamens and carpels numerous, arranged spirally: seed containing endosperm. Woody trees or shrubs.

Tribe 1. *Magnolieæ.* Carpels very numerous on an elongated cylindrical receptacle: flowers invested by a spathoid bract; stipules connate. *Magnolia grandiflora* and other species, and *Liriodendron tulipifera*, the Tulip-tree, from North America, are ornamental trees.

Tribe 2. *Illicieæ.* Carpels in a single whorl on a flat receptacle (Fig. 340). *Illicium anisatum*, the Star-Anise, is a native of China.

Order 3. CALYCANTHACEÆ. Flowers acyclic, perigynous: fruit, an etærio of achenes, resembling that of the Rose.

Calycanthus floridus, Carolina Allspice, is an ornamental shrub with brown aromatic flowers. Chimonanthus, a fragrant shrub, also belongs here.

Order 4. NYMPHÆACEÆ. Flowers usually acyclic without any sharp demarcation between the petals and the stamens: pistil either apo- or syn-carpous. Water-plants, generally with broad floating leaves.

Tribe 1. *Nymphæinæ.* Carpels connate, forming a polymerous multilocular ovary which may be either superior or inferior. Ovules numerous, placentation superficial: seeds numerous, containing both endosperm and perisperm, sometimes arillate (p. 459). The rhizome grows at the bottom of the water and throws up broad, flat, cordate leaves with long petioles which float on the surface. The flower also reaches the surface, borne on a long peduncle.

Nymphæa alba, the white Water-Lily, has four green sepals, a great number of white petals which, together with the very numerous stamens, are arranged spirally, and a semi-inferior ovary, *Nuphar luteum*, the yellow Water-Lily, has a calyx consisting usually of five greenish-yellow sepals; the petals, which are smaller and yellow, are usually 13 in number, and form a continuous spiral with the indefinite stamens; the ovary is superior. *Victoria regia*, a Brazilian species, has peltate leaves of more than a yard in diameter.

Tribe 2. *Nelumbieæ.* Ovaries numerous, distinct, imbedded in the fleshy receptacle: seeds solitary, exalbuminous.

Nelumbium speciosum is the Lotus of Egypt and Asia.

Tribe 3. *Cabombeæ.* Flowers cyclic. Calyx and corolla each three-leaved. Stamens 3–18 or ∞. Ovaries 3–18, monomerous, each with two or three ovules attached to its walls or to the dorsal suture of the carpel. Seeds containing endosperm and perisperm. The submerged leaves are much divided, the floating leaves peltate. Cabomba occurs in tropical America: Brasenia is widely distributed.

Cohort II. **Menispermales.** Flowers usually ambisporangiate, sometimes monosporangiate and then frequently polygamous; cyclic, typically trimerous: perianth usually differentiated into calyx and corolla, and then either homochlamydeous or heterochlamydeous: stamens usually 3 or a multiple of 3: gynæceum trimerous and apocarpous or syncarpous, or monomerous; ovary unilocular, with usually a single basal or suspended anatropous or orthotropous ovule; seed with or without endosperm; endosperm sometimes ruminated.

Order 1. **Menispermaceæ.** Flowers usually diœcious, but with traces of the missing organs: perianth usually biseriate, heterochlamydeous: the calyx, corolla, and andrœcium have usually two whorls each. Carpels usually 3–6, distinct, one-seeded, but many-seeded in the sub-family Lardizalbeæ. Seed with or without endosperm. They are mostly tropical climbing plants with woody twining stems and palmate leaves.

The structure of the flower is very variable: pleiotaxy is frequent; thus the calyx may consist of 3 or more (8–10 in Sychnosepalum) whorls, the corolla of 3 whorls (occasionally in Menispermum), the andrœcium of as many as 8 whorls (Menispermum, Anamirta): on the other hand oligotaxy sometimes occurs; the corolla may be completely suppressed (*e.g.* Abuta, Akebia), and in the latter genus the calyx consists of only a single whorl. The ♂ flower of Cissampelos is dimerous, and the ♀ flower has a rudimentary perianth and a unilocular ovary with three stigmata. The endosperm is ruminated in some genera (*e.g.* Anomospermum, Abuta, Chasmanthera): the seed is exalbuminous in the Pachygoneæ (*e.g.* Pachygone, Sychnosepalum, Rameya).

Fig. 399. — Diagram of flower of many of the Menispermaceæ.

Order 2. **Berberidaceæ.** Flowers ambisporangiate: the calyx, corolla, and andrœcium, each consist of two di- or tri-merous whorls. Gynæceum monomerous; ovary with numerous marginal ovules. Fruit capsular or baccate. Seed with endosperm.

Berberis vulgaris is the Barberry; its floral formula is $K3+3$, $C3+3$, $A3+3$, $G^{\underline{(1)}}$; the flowers are in pendent racemes, usually without terminal flowers; when a terminal flower is present it is acyclic and its formula is $K5 \mid C5 \mid A5$ (see Fig. 311, p. 498). Fruit an oval berry. The leaves of the ordinary shoots are transformed into spines (Fig. 38), in the axils of which are dwarf-shoots bearing the foliage-leaves and the inflorescences. Epimedium has a dimerous flower; calyx of 4–5 whorls; petals spurred. In Berberis, sub-genus Mahonia, there are 3 whorls of sepals, and in Nandina many whorls the inner of which gradually become petaloid. Podophyllum has sometimes 3 whorls of petals (though the number of petals varies in consequence of oligomery), and shows duplication of the stamens of the inner whorl. The anthers usually dehisce by valves, but in Podophyllum and Nandina the dehiscence is longitudinal.

Order 3. LAURACEÆ. Flowers ambisporangiate, or polygamous, somewhat perigynous, usually trimerous (sometimes dimerous or tetramerous): perianth sepaloid, in two whorls: stamens 9–12, in three or four whorls, those of one or more whorls being frequently staminodes; the anthers open by 2 or 4 valves, the outer introrse, the inner extrorse; the filaments have glandular appendages (Fig. 400 *b b*). Ovary trimerous, unilocular, with one suspended ovule, two of the three loculi being abortive. Fruit a berry or a drupe. Seed devoid of endosperm.

This order is frequently placed in the sub-class Monochlamydeæ; but there can be no doubt that such a position is unsatisfactory: the order seems rather to be allied to the Menispermaceæ. The chief morphological difficulty is the interpretation of the perianth; since it consists of two whorls, and is homochlamydeous and sepaloid, it may be regarded as corresponding to the two-whorled calyx of other Menispermales; from this point of view the Lauraceæ would be held to have no corolla: on the other hand, the fact that the two whorls are developed differently, the segments of the outer whorl being developed successively and those of the inner whorl simultaneously, tends to prove that the outer whorl is a calyx and the inner whorl a corolla. In *Laurus nobilis* what appear to be petals are exceptionally present in addition to the two normal perianth-whorls; but these petals are really staminodes, due to petaloid metamorphosis of the four stamens of the external whorl.

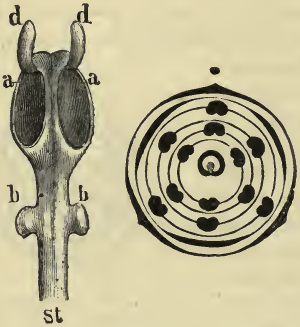

FIG. 400.—Stamen of Laurus. Anthers opened, *a a*; *d d* the valves; *b b* glandular appendages. Diagram of Cinnamomum.

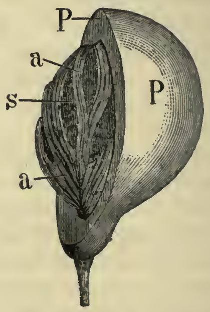

FIG. 401.—Fruit of the Nutmeg-tree, *Myristica moschata*. *P* Pericarp, half of it removed; *s* the seed; *a* aril (nat. size).

These are usually evergreen shrubs with coriaceous leaves (*e.g. Laurus nobilis*, the Sweet Bay); a few, as Cassytha, are parasites resembling the Dodder in habit. The flowers of the Bay are diclinous.

Order 4. MYRISTICACEÆ. Flowers diœcious, perianth of a single whorl, gamophyllous, 3-lobed. Stamens 3–18 coherent into one bundle. Ovary monomerous, with one basal anatropous ovule : fruit a fleshy two-valved capsule : seed with ruminated endosperm.

Myristica moschata, the Nutmeg, is a native of New Guinea. The seed is invested by an aril (see p. 459), an integument which is developed after fertilisation ; it has a netted or laciniate appearance (Fig. 401 *a*) ; it is known in commerce as Mace. Seed large, with abundant ruminated endosperm ; the innermost layer of the brown testa closely follows all the windings, and this gives the endosperm a marbled appearance.

The affinities of this order are doubtful : it is commonly regarded as closely allied to the Lauraceæ.

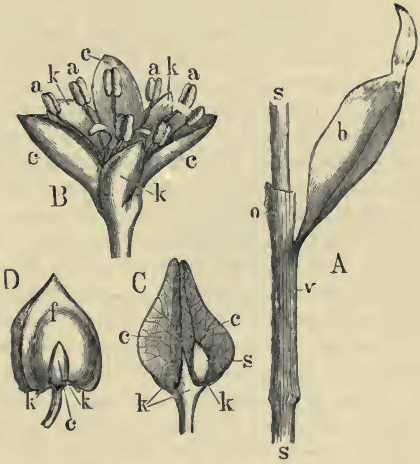

FIG. 402.—*A* Portion of the stem (*s*) of Polygonm, with a leaf (*b*), its sheath (*v*), and the ocrea (*o*) (nat. size). *B* Flower of Rheum : *k* external, *c* internal perianth-whorl; *a* the stamens. *C* Fruit of Rumex, enclosed by the inner whorl of the perianth *c* ; *s* dorsal ridge of one of the perianth-leaves ; *k* external perianth-leaves. *D* fruit of Rheum (*f*) : *k* outer, *c* inner perianth-whorl (enlarged).

Order 5. POLYGONACEÆ. Flowers ambisporangiate, sometimes monosporangiate by suppression, trimerous (sometimes dimerous), with the typical formula $K\,3$, $C\,3$, $A\,3+3$, $G\,(3)$: perianth in two whorls, homochlamydeous, either sepaloid or petaloid, sometimes reduced to 5 leaves : stamens in usually two regularly alternating whorls ; the number of stamens in the outer whorl is frequently increased by duplication ; the number of the stamens is frequently reduced by suppression. Ovary usually trimerous, unilocular, with a single basal orthotropous ovule. The fruit is more or less enveloped by the persistent perianth (Fig. 402 *C*). The seed contains endosperm, in which the straight or curved embryo is imbedded. The leaves have sheathing bases, and connate stipules (Fig. 402 *A*), forming an ocrea (see p. 48) which embraces the stem for some distance above the leaf-sheath (absent in Eriogonum).

This order, like the Lauraceæ, is commonly placed in the Monochlamydeæ, and the interpretation of the two-whorled perianth presents the same difficulty and may be regarded from the two points of view in both orders (see Lauraceæ).

The typical structure of the flower is to be found in the genus Pterostegia. As regards the perianth, it is dimerous in Oxyria, it is 5-leaved in most species of Polygonum, in Coccoloba, Muehlenbeckia, etc., and is apparently quincuncial ($\frac{2}{5}$); however, the development of the flower shows that this is not really the case, but that it is the result of reduction by the absence of the anterior segment of the inner perianth-whorl: it may be mentioned further that when the perianth is trimerous, there is (if any) but a single prophyllum, whereas when it is pentamerous there are two prophylla. As regards the andrœcium, in a trimerous flower, only a single whorl of stamens may be developed; either the outer (*e.g.* Rumex, Kœnigia, as also in the dimerous flower of *Polygonum diospyrifolium*), or the inner (Leptogonum). Duplication obtains in the single whorl of stamens of Rumex and *Polygonum diospyrifolium*, and in the outer whorl of many genera, in which either all the typical number of stamens are duplicated (*e.g.* Rheum, Oxyria), or some only (*e.g.* species of Polygonum, in which also suppression is frequent). It is important to note that the number (usually 5–8) of stamens in a flower with a pentamerous perianth bears no direct relation to the number of the perianth-leaves; whereas in dimerous flowers the number of the stamens is a multiple of 2. In some rare cases the number of the stamens is large (12–50). When two whorls of stamens are present, the outer being duplicated, it is frequently the case (*e.g.* species of Polygonum) that the anthers of the external stamens are introrse and those of the inner stamens extrorse. The gynæceum is sometimes dimerous when the perianth is pentamerous (*e.g. Polygonum orientale*, *amphibium* and other species); always when the perianth is dimerous. The endosperm is sometimes ruminated (Coccoloba). The British genera are the following:—Polygonum, the Bistort or Knot-Grass, of which there are many species (*e.g. Bistorta*, *Hydropiper*, *Persicaria*, *amphibium*, *aviculare*, *Convolvulus*); Rumex, the Dock or Sorrel, the leaves of which contain a large quantity of oxalic acid; Oxyria, the Mountain Sorrel.

The most important economic plants are:—Rheum, the Rhubarb; the Rhubarb of the pharmacopœia is obtained from *R. palmatum tanguticum* and *R. officinale* (China); the garden Rhubarbs are *R. rhaponticum* and *undulatum*: *Fagopyrum esculentum*, the Buckwheat.

Order 6. CERATOPHYLLACEÆ. Submerged water-weeds of doubtful affinity, with whorled sessile leaves dichotomously branched and subdivided; in the axils of some of these the diclinous flowers occur. The ♂ flowers consist of from 6–12 perianth-leaves and about as many stamens; the ♀ flowers have a similar perianth and a monomerous ovary with a single suspended orthotropous ovule: seed with endosperm.

Ceratophyllum demersum and *submersum* occur submerged in ponds and ditches. Pollination takes place under water, and in correlation with this the wall of the pollen-grain is not cuticularised (see p. 434).

Cohort III. **Caryophyllales.** Flowers cyclic, generally actinomorphic and pentamerous, sometimes monochlamydeous: calyx often gamosepalous: stamens usually definite: ovary unilocular, with basal placenta: seed with perisperm.

Order 1. CARYOPHYLLACEÆ. Flowers generally pentamerous, with calyx and corolla, though the latter is suppressed in some cases; sepals distinct or coherent: stamens in two whorls (see p. 503), of which the inner is often wanting; ovary 2-, 3-, or 5-merous, unilocular, or multilocular at the base, with a central placenta or with a single basal ovule: fruit usually a capsule: leaves opposite, decussate: stems usually tumid at the nodes.

Tribe 1. *Alsineæ.* The corolla and the inner whorl of stamens are usually present; the calyx is eleutherosepalous; fruit a capsule; usually no stipules.

The British genera are Sagina (Pearl-wort), Arenaria (Sandwort), Cerastium, Stellaria (Chick-weeds and Stitch-worts), Spergula (Spurrey), Lepigonum, Holosteum, Mœnchia; they are mostly small herbaceous plants with white petals, occurring in meadows, on roadsides, etc., but species of Lepigonum (Spergularia), the Sandwort-Spurrey, and *Arenaria* (*Honckenya*) *peploides*, Sea-Purslane, grow on the sea-coast; they are distinguished from each other principally by the number of carpels present, and by the mode of dehiscence of the fruit.

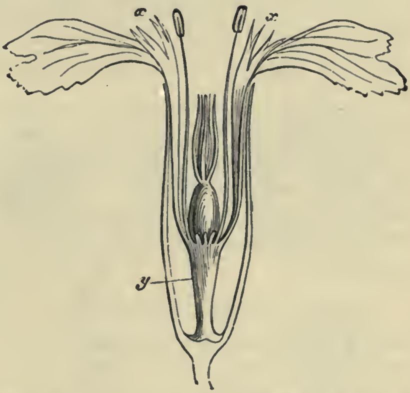

FIG. 403.—Longitudinal section of the flower of *Lychnis Flos Jovis*: *y* prolonged axis (anthophore; see p. 494) between the calyx and the corolla; *x* ligular appendages or corona. (After Sachs.)

Tribe 2. *Sileneæ.* The corolla and the inner whorl of stamens are always present: the calyx is gamosepalous; stamens 10, filaments connate at base: the fruit is a capsule (in Cucubalus a berry): the leaves have no stipules; the floral axis is often elongated between the calyx and the corolla (Fig. 403 *y*): the petals (as in Lychnis and Saponaria) often have ligular appendages (Fig. 403 *x*: see p. 515).

The species of Dianthus, the Pink, which commonly occur wild are *D. deltoides*, *D. cæsius* and *D. Armeria; D. Caryophyllus*, the Carnation, and *D. chinensis*, are well-known garden flowers: there are two styles, and the calyx is surrounded at its base by bracteoles. The genus Saponaria has two styles but no bracteoles; *S. officinalis*, the Soap-wort, occurs on the banks of rivers. The genus Silene (Catchfly) has three styles; *S. inflata*, *nutans*, and others, are common in meadows. The genus Lychnis (Campion) has five styles; the species *alba* (*vespertina*) and *diurna* are diœcious; *L. Githago*, the Corn-cockle, is common in fields.

Tribe 3. *Polycarpeæ*. Leaves with scarious stipules: calyx eleutherosepalous; the corolla is present, but the inner whorl of stamens is wanting: style 3-fid. This group includes the British genus Polycarpon (Allseed) and others.

Tribe 4. *Paronychieæ*. Sepals distinct or coherent: the corolla and the inner whorl of stamens are usually wanting: style usually bifid: ovary unilocular, with 1–4 ovules: fruit generally indehiscent.

The British genera are Scleranthus (Knawel), Herniaria, Corrigiola (Strapwort), and Illecebrum: they are small inconspicuous herbs, with scarious stipules (except Scleranthus).

The Paronychieæ have also been placed, as a distinct natural order ILLECEBRACEÆ, among the Monochlamydeæ. There is no doubt that they have affinities with the Chenopodiales, and that they thus connect that cohort with the Caryophylleæ.

Order 2. PORTULACEÆ. Calyx usually of 2 sepals and corolla of 5 petals: stamens usually 5, antipetalous: ovary usually trimerous and unilocular; fruit a capsule. They are herbs with alternate or opposite leaves; the corolla is fugacious.

The structure of the flower is essentially the same in this order as in the Chenopodiales, with the addition of a calyx of two antero-posterior sepals.

Portulaca oleracea, the Purslane, from Southern Europe, and other species are cultivated as vegetables and as ornamental plants. Montia (Blinks) has an irregular (apparently gamopetalous) corolla; it grows in ditches or in damp places. In the genus Lewisia there are 4–8 sepals, 8–16 petals, and indefinite stamens.

Order 3. AIZOACEÆ (FICOIDEÆ). Flowers with a simple perianth, and usually indefinite stamens, the more external of which are often transformed into petaloid staminodes: ovary multilocular, sometimes inferior.

This order has marked affinities with the Phytolaccaceæ and the Nyctaginaceæ, so that it is sometimes placed among the Monochlamydeæ; but the occurrence of forms with petaloid staminodes justifies the position in which it is here placed. It is of special interest inasmuch as it well illustrates the evolution of the dichlamydeous from the monochlamydeous type of flower, with multiplication of the sporophylls and the gradual metamorphosis of the more external of them into petaloid staminodes which are, in fact, primitive petals.

Mesembryanthemum is the genus with an inferior ovary: it has fleshy leaves and conspicuous flowers; many species are cultivated; it comes from South Africa.

Cohort IV. **Parietales.** Flowers cyclic, with calyx and corolla: sepals free: stamens definite or indefinite: gynæceum of two or more carpels: ovary unilocular, sometimes many-chambered, with parietal placentation: seed with or without endosperm.

Order 1. PAPAVERACEÆ. Flowers usually actinomorphic, $K2$,

$C2+2$, $A\infty$, $G^{(2)}$ or (∞), or rarely with trimerous whorls: calyx sepaloid, corolla petaloid: the numerous whorls of stamens alternate: ovary of two lateral carpels or of more (Fig. 404 *a*), two- or more-chambered: ovules numerous, attached to the more or less infolded edges of the carpels: endosperm abundant, embryo small. The sepals commonly fall off before the flower expands (Fig. 404 *k*). Plants with abundant milky latex.

Papaver, the Poppy, has a many-chambered ovary; the fruit is a porous capsule (Fig. 342 *D*): *P. somniferum* is cultivated for the sake of the oil contained in the seeds, and for the latex obtained from its capsules, which, when inspissated, constitutes opium: several species are British, such as *P. Rhœas*, the Field Poppy; *P. Argemone*, the Pale or Long Prickly-headed Poppy; *P. hybridum*, the Round Prickly-headed Poppy; *P. dubium*, the Long Smooth-headed Poppy; and *Meconopsis cambrica*, the Yellow Welsh Poppy. *Chelidonium majus*, the Celandine, has two carpels, a siliquose fruit, and orange-coloured milky latex. Glaucium, the Horned Poppy, has a siliquose fruit which is generally spuriously bilocular. *Eschscholtzia californica* is a cultivated plant; it has a hollow receptacle, so that its flowers are almost perigynous.

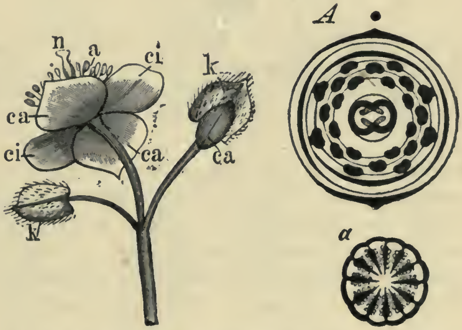

FIG. 404.—Flower of *Chelidonium majus* (nat. size); *k* calyx; *ca* outer, *ci* inner petals; *a* stamens; *n* stigma. *A* Diagram of the flower of Chelidonium. *a* Many-chambered ovary of Papaver.

Order 2. FUMARIACEÆ. Flowers isobilaterally symmetrical, or zygomorphic with lateral symmetry: floral formula $K2$, $C2+2$, $A2+2$, $G^{(2)}$. The three whorls of the perianth alternate; one of the outer petals (rarely both) is usually furnished with a spur: in most genera there are three stamens on each side, a central one, with a perfect anther (the stamen of the outer whorl, Fig. 405 *B a*), and two lateral stamens, each with only half an anther (apparently the halves of the stamens of the inner whorl; Fig. 405 $B\,a_{,}\,a_{,}$). The fruit is siliquose and many-seeded, or one-seeded and indehiscent. Herbaceous plants without milky latex, sometimes climbing by means of their petioles which act as tendrils (Adlumia, Fumaria). Seeds containing endosperm.

The flowers of Adlumia, Dicentra, and Hypecoum are isobilaterally symmetrical. *Dicentra spectabilis* is a favourite ornamental plant; both the outer petals are spurred, the two inner petals are hollowed at their apices, so that they completely enclose the anthers. In Hypecoum the flower is isobilaterally symmetrical, but the petals are not spurred, and there are four stamens, two lateral forming the outer whorl, and two antero-posterior forming the inner whorl: fruit usually indehiscent. In Corydalis and Fumaria only one of the outer petals is spurred, and consequently the flower is irregular and laterally zygomorphic. In Corydalis the fruit is a two-valved capsule with numerous parietal seeds: some species, *e.g. C. cava* and *solida*, have a tuberous rootstock; others, as *C. lutea* and *aurea*, have rhizomes. *Fumaria officinalis* and others (Fumitories) are common in fields; the ovaries contain but few ovules, and of these only one ripens to a seed; fruit globose, indehiscent.

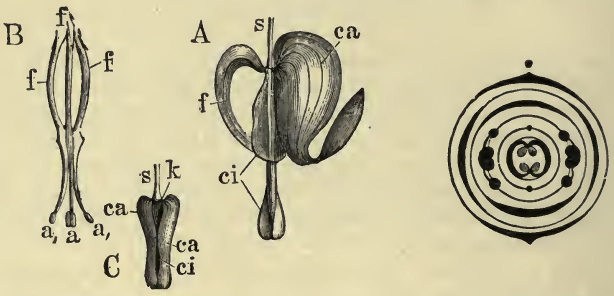

FIG. 405.—*A* Flower of *Dicentra spectabilis*: one of the outer petals is removed: *s* pedicel; *ca* the outer, *ci* the inner petals; *f* stamens. *B* The three stamens of one side, seen from within: *f* filaments; *a* the middle complete anther; *a, a,* the lateral half-anthers. *C* Flower-bud, with the sepals, which soon fall off, still adhering (*k*); (nat. size). Diagram of Fumitory.

Order 3. CRUCIFERÆ. Flowers regular, isobilateral: floral formula $K2+2$, $C\times 4$, $A2+2^2$, $G^{(2)}$. The four petals form a whorl, alternating with the four sepals as if the latter formed one whorl; there are, however, three perianth-whorls, as in the two preceding families; but whereas in them only the outermost whorl is sepaloid, in this family the two outer whorls are sepaloid, and the innermost, which alone is petaloid, is a whorl consisting of four instead of two members. The two outer stamens are lateral, as in those families; the two inner ones, which in most Fumariaceæ are apparently divided, are here duplicate, having longer filaments (Fig. 407 *B b b*) than the outer ones (*a*); hence the flower is *tetradynamous.* There are usually four, sometimes more, glands at the

FIG. 406.—Diagram of the flower of Cruciferæ.

base of the stamens (Fig 407 *B d*). The ovary consists of two carpels with the ovules in two longitudinal rows on the connate margins of the carpels; these two parietal placentæ are connected by a membranous growth which, as it is not formed of the margins of the carpels, must be regarded as a spurious dissepiment (Figs. 407 D* E* *v*, 342 *C w*). When the fruit opens, the pericarp splits into two valves corresponding to the carpels, leaving their margins, as a frame or *replum*, bearing the placentæ with the spurious dissepiment attached: the seeds remain attached to them for some time (Fig. 342 *C*, p. 530).

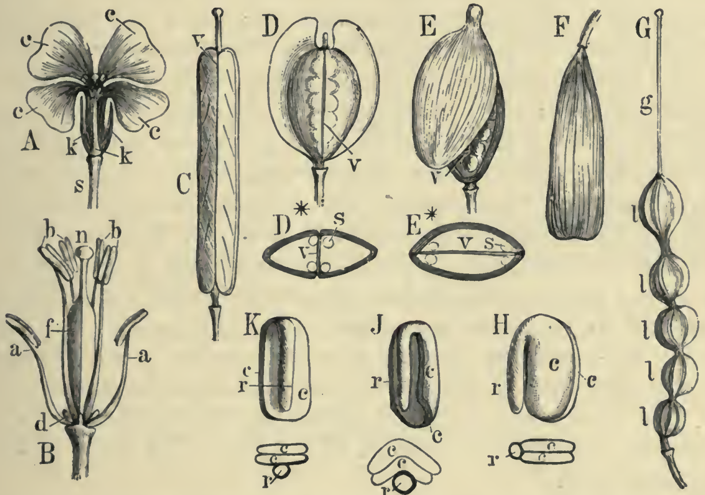

Fig. 407.—Flowers, fruits, and embryos of various Cruciferæ. *A* Flower of Brassica (nat. size); *s* pedicel; *k k* calyx; *c* corolla. *B* The same after removal of the perianth (much mag.): *a a* the two outer short stamens; *b* the four longer inner ones; *f* the ovary; *n* the stigma; *d* gland. *C* Siliqua of Brassica: *v* dissepiment. *D* Angustiseptal silicula of Thlaspi. *E* Latiseptal silicula of Draba. D* and E* Diagrammatic transverse section of the preceding: *v* dissepiment; *s* seed. *F* Indehiscent silicula of Isatis. *G* Jointed siliqua of *Raphanus Raphanistrum*: *g* style; *l l l* separate segments. *K–H* Diagrams of differently-folded embryos, with transverse sections: *r* radicles; *c c* cotyledons.

The flowers are in racemes in which the bracts are suppressed; when the lower pedicels are longer than the upper ones, the raceme becomes a corymb, and then the lower flowers are usually zygomorphic, the petals turned towards the periphery being larger than those directed towards the axis of the inflorescence, as in Iberis.

The form of the fruit is of importance in the subdivision of this order. In some genera it is much longer than it is broad, when it is termed a *siliqua*, (Figs. 407 *C*, 342 *C*); in others, it is not much longer, or about as long as it is broad, when it is termed a *silicula* (Fig. 407 *D* and *E*). The latter is commonly somewhat compressed in one direction; either parallel to the dissepiment, that is to say laterally (Fig. 407 *E* and *E**), so that the dissepiment lies in the direction of the greatest diameter, when it is *latiseptal*; or perpendicularly to the dissepiment, that is in the median plane, so that the dissepiment lies in the narrowest diameter, when it is *angustiseptal* (*D* and *D**). Fruits with only one or a few seeds, and which are indehiscent, are confined to only a few genera, such as Isatis (Fig. 407 *F*). So likewise is the jointed siliqua, which has transverse dissepiments between the seeds; when they are ripe it divides transversely into segments, as in Raphanus (Fig. 407 *G*).

The seed is exalbuminous. The embryo is folded in the seed in various ways; the radicle may lie in the same plane as one of flat cotyledons (Fig. 407 *K*), when the cotyledons are said to be *incumbent*, *Notorhizeæ* (the diagram being ○ ||); or the radicle may occupy the same position, the cotyledons being folded (Fig. 407 *J*), when the cotyledons are said to be *incumbent* and *folded*, *Orthoploceæ* (diagram of section ○ ≫); or, thirdly, the radicle may be lateral to the two cotyledons (Fig. 407 *H*), when the cotyledons are said to be *accumbent*, *Pleurorhizeæ* (diagram ○ =): more rarely the cotyledons are spirally rolled so that in a transverse section they are cut through twice, *Spirolobeæ* (diagram ○ || ||); or, finally, they may be doubly folded, and be seen four times in a section, *Diplocolobeæ* (diagram ○ || || || ||). The seeds contain much fatty oil.

Sub-order 1. SILIQUOSÆ. Fruit a siliqua, much longer than it is broad.

Tribe 1. *Arabideæ.* ○ =. *Cheiranthus Cheiri*, the Wall-flower, and *Matthiola annua* and *incana*, the Stocks, are cultivated as garden-plants. *Nasturtium officinale* is the Water-cress. *Barbarea vulgaris* is the Yellow Rocket. Cardamine (incl. Dentaria) also belongs to this tribe.

Tribe 2. *Sisymbrieæ.* ○ ||. *Sisymbrium officinale*, the Hedge-Mustard, is common on rubbish heaps; and Erysimum, the Treacle-Mustard, on walls, etc. Hesperis is the Dame's Violet.

Tribe 3. *Brassiceæ.* ○ ≫. The species and varieties of Brassica are much cultivated. *Brassica oleracea* is the Cabbage, with the following varieties; *acephala*, Scotch kale, Cow-cabbage or Borecole; *bullata*, the Savoy-cabbage; *capitata*, the red and white Cabbage; *caulorapa*, with the stem swollen at the base, is the Kohl-rabi; *Botrytis*, with connate fleshy peduncles and abortive flowers, is the Broccoli (*asparagoides*) and the Cauliflower (*cauliflora*); *gemmifera*, with numerous lateral leaf-buds, known as Brussels-sprouts. *Brassica campestris* is the wild Navew; it includes the following sub-species: *Rapa*, the wild Turnip, with bright green hispid leaves and flat corymbs of flowers, among the cultivated varieties of which is the var. *depressa*, the Turnip: *Napus*, the wild Rape, with glabrous glaucous leaves and long racemes of flowers, several varieties of which are cultivated for their oily seeds, and one (var. *esculenta*, the Teltow Turnip) for its fleshy root: *Napobrassica*, the Turnip-cabbage, including *Rutabaga*, the Swedish Turnip. *B. campestris oleifera* is the true Colza or Coleseed, from the seeds of which colza-oil is obtained. *Brassica* (*Sinapis*) *nigra* and *alba* are the black and white Mustard. *Brassica Sinapis* (*Sinapis arvensis*) is the Charlock or Corn-Mustard. To this tribe belongs also the genus Diplotaxis.

Sub-order 2. SILICULOSÆ. Fruit a silicula.

A. *Latiseptæ.* The dissepiment is in the longest diameter of the silicula.

Tribe 4. *Alyssineæ.* ○ =. *Cochlearia officinalis* is the Scurvy-grass; *C. Armoracia*, the Horse-radish, has a thickened root. *Alyssum calycinum* and *Draba* (*Erophila*) *verna*, the Whitlow-grass (Fig. 407 *E*), are common weeds: *Lunaria biennis* is Honesty.

Tribe 5. *Camelineæ.* ○ ‖. To this tribe belong Camelina (Gold-of-pleasure), and Subularia, the Awl-wort, an aquatic plant.

B. *Angustiseptæ.* The dissepiment is in the shortest diameter of the silicula.

Tribe 6. *Lepidineæ.* ○ ‖. *Capsella Bursa Pastoris*, the Shepherd's Purse, is common, as also various species of Senebiera and Lepidium (Cresses).

Tribe 7. *Thlaspideæ.* ○ =. Various species of Thlaspi, the Penny-Cress, are common. To this tribe belong also the British genera Iberis (Candytuft), Teesdalia, and Hutchinsia.

Sub-order 3. NUCUMENTACEÆ. Silicula indehiscent, few-seeded.

Tribe 8. *Isatideæ.* *Isatis tinctoria*, the Woad, has compressed, pendulous, unilocular, one-seeded fruits (Fig. 407 *F*): the leaves yield a blue dye.

Sub-order 4. LOMENTACEÆ. Fruit a siliqua or silicula, constricted into one-seeded segments (*lomentaceous*) (Fig. 407 *G*).

Tribe 9. *Cakilineæ.* Silicula two-jointed. This tribe contains the genera Cakile, the Sea-Rocket, and Crambe, the Sea-Kale.

Tribe 10. *Raphaneæ.* Silicula more or less moniliform. *Raphanus sativus* is the Radish; *R. Raphanistrum*, the Wild Radish or White Charlock, is a common weed.

Order 4. CAPPARIDACEÆ. Flower isobilateral; formula $K2+2$, $C\times 4$, $A2+2^2$ or ∞, $G^{\underline{(2)}}$ or ∞: stamens 4 or more, when 6 very rarely tetradynamous: gynæceum borne on a special prolongation of the axis (gynophore, p. 495) (Fig. 408 *t*). Fruit a siliqua or a berry.

FIG. 408.—Flower of *Capparis spinosa* (nat. size): *s* pedicel; *k* calyx; *c* corolla; *a* stamens; *f* gynæceum on (*t*) gynophore.

The flower-buds of *Capparis spinosa* from the South of Europe are known as Capers.

Order 5. **Resedaceæ.** Flowers irregular, dorsiventral: sepals and petals 5–8, the latter laciniate: stamens numerous: carpels 2–6 connate, forming a unilocular ovary, open at the apex, with numerous ovules; seed without endosperm: inflorescence a raceme, without bracteoles.

Reseda Luteola, the Dyer's Weed, or Weld, yields a yellow dye; *R. odorata* is Mignonette.

Order 6. **Cistaceæ.** Flowers usually actinomorphic and pentamerous: the two external of the five sepals are generally smaller, and sometimes they are absent: stamens numerous, in consequence of multiplication: carpels 3–10, forming a uni- or multilocular ovary; ovules orthotropous; seed with endosperm. Trees or shrubs with generally opposite stipulate leaves.

Cistus has 5-10 carpels forming a chambered or completely multilocular ovary. *Cistus ladaniferus*, *creticus*, and other species, grow in the south of Europe; a balsam is derived from them. Helianthemum has a unilocular trimerous ovary: *Helianthemum vulgare*, the Rock Rose, is an under-shrub which grows wild on dry soils.

Order 7. **Bixaceæ.** The seed of *Bixa orellana*, a native of America, yields an orange-coloured dye known in commerce as Annatto.

Order 8. **Violaceæ.** Floral formula $K5$, $C5$, $A5$, $G^{\underline{(3)}}$: flowers always borne laterally: ovules anatropous: fruit a loculicidal capsule (Fig. 409 *C*): seed with endosperm. The indigenous species have irregular dorsiventral flowers; the anterior inferior petal is prolonged into a hollow spur (Fig. 409 *A cs*) in which the nectar secreted by the spur-like appendages of the two lower stamens collects (Fig. 409 *A fs*). The sepals are produced at the base (Fig. 409 *A ls*).

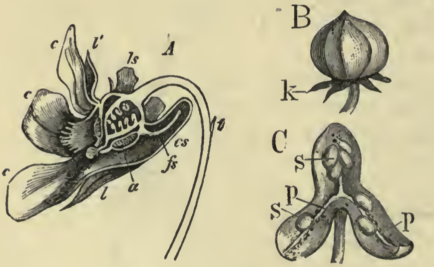

Fig. 409.—*Viola tricolor*. *A* Longitudinal section of flower: *v* bracteole on the peduncle; *l* sepals; *ls* appendage; *c* petals; *cs* spur of the lower petals; *fs* glandular appendage of the lower stamens; *a* anthers (after Sachs). *B* Ripe fruit; *k* calyx. *C* After dehiscence: *p* parietal placentæ; *s* seeds. (Mag.)

Viola is the Violet, Pansy, or Heart's-ease:—many species, as *V. odorata*, the Sweet Violet, have only an underground stem which bears cataphyllary leaves, and which throws up petiolate foliage-leaves, and bracteolate peduncles each bearing a single flower: *V. odorata* has runners, but *hirta* and *collina* have none:—in others, as *V. canina*, the Dog-Violet, the main stem is above ground and bears the foliage-leaves:—in *V. mirabilis* these two forms are so combined that, in the spring, flowers are developed from the rhizome which have large blue petals but are always sterile; it is not till later that inconspicuous (cleistogamous, p. 453) flowers with minute petals appear on the leafy stem, and these only are fertile:—in *V. tricolor* and its allies the stipules are leafy and pinnatifid.

Cohort V. **Sarraceniales.** Flowers regular, generally actinomorphic, sometimes monochlamydeous: stamens often numerous, ovary syncarpous, uni- or multi-locular; placentation various; seeds many, with endosperm; leaves adapted in various ways for the capture of insects.

Order 1. SARRACENIACEÆ. Flowers ☿, usually dichlamydeous, hemicyclic: stamens 15 or more: ovary either unilocular and more or less chambered, or 3- or 5-locular; placentation parietal or axile: leaves pitchered (Fig. 410).

This order includes the three herbaceous genera Sarracenia, Darlingtonia, and Heliamphora. The two former have pentamerous dichlamydeous flowers, each borne singly on a peduncle; the sepals and petals are in $\frac{2}{5}$ arrangement, and the stamens are indefinite in Sarracenia and 15 in Darlingtonia; carpels 5, antisepalous in Sarracenia, antipetalous in Darlingtonia: they grow on moors and marshes in North America. Heliamphora bears its flowers in racemes; the flower has a simple petaloid perianth, indefinite stamens, and a trilocular ovary; it is a native of British Guiana.

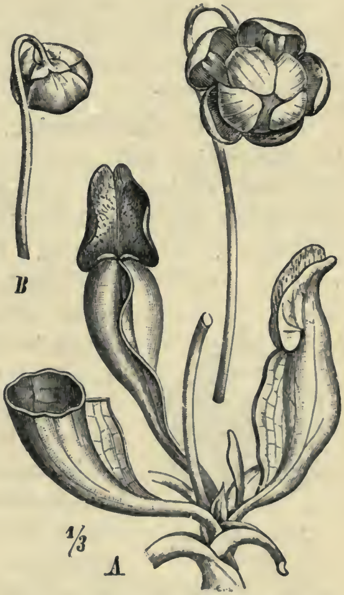

FIG. 410.—Leaves and flowers of *Sarracenia purpurea* ($\frac{1}{3}$): the leaf to the left has been cut across.

Order 2. NEPENTHACEÆ. Flowers diœcious, monochlamydeous, tetramerous: stamens generally 4–16, coherent into a central column: ovary quadrilocular, with axile or somewhat superficial placentation: leaves pitchered (Fig. 37, p. 58).

This tropical order includes the single genus Nepenthes, with about 40 species, chiefly inhabiting the Malay Archipelago, but extending to Ceylon, Australia, the Seychelles, and Madagascar: they are mostly climbing shrubs with leaf-tendrils.

Order 3. DROSERACEÆ. Flowers ☿, dichlamydeous, generally pentamerous: stamens 5 or 5^n: carpels 2–5; ovary usually unilocular with parietal placentæ: leaves not pitchered.

Herbaceous plants, constituting the six genera Dionæa, Aldrovanda, Roridula, Byblis, Drosera (the Sundew) and Drosophyllum: in Dionæa, Aldrovanda, and Drosophyllum, the gynæceum consists of 5 antipetalous carpels, and the ovary is unilocular; in Drosera and Roridula the gynæceum is usually trimerous, the ovary unilocular in the former, trilocular in the latter; in Byblis it is dimerous and bilocular. The leaf-blade of Dionæa (Venus' fly-trap) and of Aldrovanda is sensitive to touch, the two halves closing sharply along the middle line when irritated: the leaves of the other genera are provided with irritable glandular tentacles (see Figs. 42, 43, p. 66). Aldrovanda (*A. vesiculosa*) is a rootless, floating water-plant.

Cohort VI. **Guttiferales**. Flowers usually cyclic, generally actinomorphic, and pentamerous: sepals usually free, with imbricate æstivation: stamens usually indefinite: gynæceum syncarpous, ovary uni- or multi-locular: seed exalbuminous.

Order 1. HYPERICACEÆ. Formula usually $K5$, $C5$, $A0+5\infty$, $G^{(5)}$; or $A0+3\infty$, $G^{(3)}$. Sepals sometimes united at the base: stamens usually indefinite and polyadelphous; when in five bundles, the bundles are superposed on the petals; this position of the stamens is generally attributed to the suppression of an outer whorl of stamens which is indicated by staminodes in species of all the genera: ovary uni- or multi-locular, or many-chambered; capsule septicidal; ovules numerous, anatropous; placentæ parietal or axile. Herbs or under-shrubs with decussate entire leaves, which are dotted over with translucent oil-glands; exstipulate.

FIG. 411.—Diagram of Hypericum.

The following are examples of the different relative numbers of staminal bundles and of carpels:—

Staminal bundles 5, carpels 5: *Hypericum calycinum.*
Staminal bundles 3, carpels 3: *H. humifusum, hirsutum, montanum, perforatum, undulatum, barbatum.*
Staminal bundles 5, carpels 3: *H. Androsæmum, hircinum, elatum.*
Staminal bundles 3, carpels 5: *H. peplidifolium.*

All these species, except the last (St. John's Worts, or Tutsans), occur wild in Britain.

Order 2. TAMARICACEÆ. Flowers 4- or 5-merous, with one or two whorls of stamens: calyx gamosepalous: ovary usually trimerous, unilocular, with basal or parietal placentation: capsule loculicidal: seeds with hairs: flowers in racemes or spikes.

This order includes the shrubs known as Tamarisks: Myricaria, Tamarix, Reaumuria, and Fouquiera. *Myricaria* (*Tamarix*) *germanica* has monadelphous stamens. *Tamarix gallica* (or *T. anglica*) has become naturalised in England.

Closely allied with this order and with the Elatinaceæ is the small order of FRANKENIACEÆ; the flower resembles that of Tamarix in the gamosepalous calyx and in the morphology of the gynæceum: *Frankenia lævis*, the Sea-Heath, occurs in salt-marshes in Britain.

Order 3. ELATINACEÆ. Small water-plants, with entire stipulate leaves opposite or in whorls: flowers 3–4-merous; formula Kn, Cn, An + n, $G^{(\underline{n})}$; solitary, without bracteoles, borne in the axils of the foliage-leaves: ovary multilocular.

E. hexandra and *Hydropiper* (Waterworts, or Water-peppers) occur, but not commonly, on the margins of lakes in England.

Order 4. TERNSTRŒMIACEÆ. Perianth spiral; the calyx is not clearly distinguishable from the numerous bracteoles: stamens indefinite: ovary multilocular. Trees or shrubs with scattered, generally coriaceous, entire leaves, without stipules.

Camellia japonica is a favourite ornamental shrub: *Thea chinensis*, of which the dried leaves are tea; black and green tea are varieties resulting only from the mode of drying the leaf.

Order 5. CLUSIACEÆ (GUTTIFERÆ). Trees or shrubs with diclinous flowers.

Order 6. DIPTEROCARPACEÆ. Trees: leaves usually stipulate: the gamosepalous calyx enlarges very much during the ripening of the fruit.

Dryobalanops Camphora, a native of Sumatra, yields the Borneo Camphor.

Cohort VII. **Malvales.** Flowers cyclic, generally pentamerous and actinomorphic: calyx often gamosepalous, with valvate æstivation: corolla with usually contorted æstivation: stamens typically in two whorls, frequently obdiplostemonous, sometimes branched, and often connate: carpels usually five and then antipetalous, often forming a multilocular ovary: seed usually with endosperm.

Order 1. TILIACEÆ. Sepals usually free: stamens 10 or indefinite, sometimes polyadelphous; in the indigenous species the staminal whorl opposite to the sepals is suppressed, and there are 5 antipetalous staminal bundles; anthers 4-locular, opening by pores or valves: gynæceum usually completely syncarpous; style 1; ovary usually 5-locular, each loculus containing two ovules; but the fruit is generally only one-seeded. Mostly trees or shrubs: leaves alternate, stipulate.

The only indigenous genus is Tilia, the Lime-tree. It has oblique leaves with deciduous stipules; the annual shoots have not a terminal bud. The inflorescence is cymose, few-flowered: the peduncle is adnate to the leafy bract; this is brought about in the following manner: in the axil of the leaves there is usually a bud, together with an inflorescence (Fig. 412): the bract (Fig 412 *h*) and the bud-scale, which is opposite to it, are the first two leaves of the axillary shoot which is terminated by the inflorescence, the peduncle of which is adnate to the bract for some distance: the bud is a winter-bud developed in the axil of the above-mentioned bud-scale. The inflorescence itself terminates in a flower; other flowers are borne in the axils of its two bracteoles, and other flowers again may be developed in the axils of their bracteoles, and so on. *T. platyphyllos*, the large-leafed Lime, has a few-flowered inflorescence, and leaves which are bright green and downy on the under surface: *T. cordata* has an inflorescence which consists of a large number of flowers, and has small leaves which are bluish-green and pubescent with red hairs on the under surface. *T. vulgaris* is the common Lime. In the American species the innermost stamens are staminodia. Corchorus, in the East Indies, yields Jute, which consists of the bast-fibres.

FIG. 412.—Inflorescence of the Lime, *Tilia platyphyllos*: *a* branch; *b* petiole with axillary bud. Attached to the peduncle is the bract (*h*): *k* calyx; *c* corolla; *s* stamens; *f* ovary; *kn* flower-bud (nat. size).

Order 2. STERCULIACEÆ.

Calyx gamosepalous: andrœcium obdiplostemonous; the stamens which are opposite to the petals are 5 or multiple, sometimes more or less monadelphous; those which are opposite to the sepals are staminodes or they are suppressed: anthers 4-locular: the corolla is sometimes wanting: gynæceum usually syncarpous, with a single style and a 5-locular ovary with 2-∞ seeds in each loculus. Flowers sometimes diclinous (Sterculieæ).

Theobromo Cacao is a tree of tropical America, the seeds of which contain a nitrogenous substance Theobromine and a fixed oil; from them Chocolate is prepared. The seeds of *ola acuminata*, a tropical African tree, have similar properties.

Order 3. MALVACEÆ. Calyx usually gamosepalous, frequently invested by an epicalyx (p. 494); the corolla is adnate at the base to the andrœcium: the typically obdiplostemonous andrœcium is a long tube (Fig. 413 *A*) consisting of five monadelphous usually branched stamens which are opposite to the petals, each branch bearing a bilocular anther; there is sometimes an inner series of staminodes opposite to the sepals: carpels 5-∞; styles many, connate; the gynæceum is sometimes almost apocarpous (Malopeæ); usually syncarpous with a multilocular ovary, splitting into cocci (Fig. 413 *C D*), with usually one ovule in each coccus (p. 530), or a loculicidal capsule (Hibisceæ), Undershrubs or herbs: leaves stipulate and generally palmately veined.

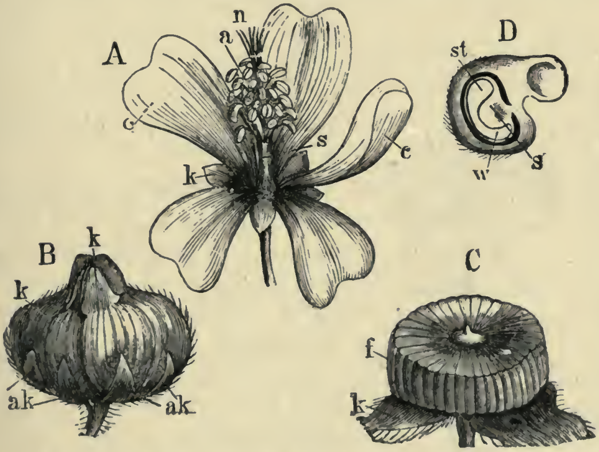

FIG. 413.—*A* Flower of *Malva Alcea* (nat. size): *k* calyx; *c* corolla; *s* connate stamens, with the anthers (*a*); *n* stigmata. *B* Fruit of *Althæa rosea* enclosed in (*k*) the calyx: *ak* epicalyx. *C* The same after the removal of the calyx. *D* A single coccus of the same in longitudinal section: *s* seed; *w* radicle; *st* cotyledon of the embryo (mag.).

Malva, the Mallow, has an epicalyx of three bracteoles, Hibiscus has one of many bracteoles, and Althæa has one of 6–9 bracteoles: *Althæa rosea* is the

Hollyhock, and *A. officinalis* is the Marsh-mallow: several species of Malva are indigenous, *M. sylvestris*, *rotundifolia*, and *moschata*: *Gossypium herbaceum* (with the vars. *religiosum* and *hirsutum*) and *G. arboreum* in Egypt and the East Indies, and *G. barbadense* (with var. *peruvianum*) in America, yield Cotton, which consists of the long hairs on the testa of the seed.

SERIES II.—DISCIFLORÆ.

Flowers typically eucyclic and generally pentamerous, often obdiplostemonous: sepals free or coherent: petals in a single whorl: stamens usually definite, and hypogynous: a disc is usually present: gynæceum generally syncarpous.

Cohort I. **Geraniales.** Flowers usually pentamerous throughout; formula $K5$, $C5$, | $A5+5$, $G^{\underline{(5)}}$; generally obdiplostemonous: the carpels are opposite to the petals: ovary usually 5-locular, with 1 or 2 suspended ovules; the micropyle is directed inwards: disc various or wanting.

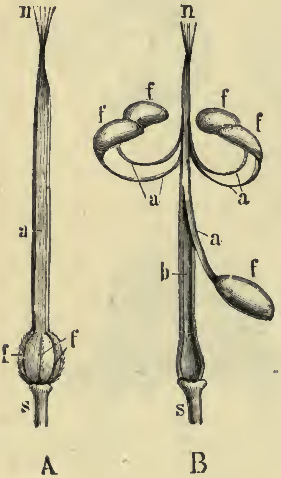

FIG. 414.—Fruit of Geranium. *A* Before, *B* after dehiscence; *s* pedicel; *f* loculi of the ovary; *a* in *B* the awn; *n* stigma; *a* and *b* carpophore. (Mag.)

Order 1. GERANIACEÆ. Disc usually represented by a gland at the base of and outside each of the antisepalous stamens: flowers usually actinomorphic: stamens connate at the base: the carpels are prolonged into a carpophore (Fig. 414 *A a*); two ovules in each loculus; the fruit is septicidal from below upwards, the awns of the separating carpels (cocci) rolling up (Fig. 414 *B*). Seed devoid of endosperm. Herbs; leaves simple, stipulate.

Geranium has 10 stamens: in most species the seed is expelled on the sudden rolling up of the awn: *Geranium pratense*, *sylvaticum*, *sanguineum*, *columbinum*, and other species, the Crane's-bills, are wild in England; *G. Robertianum*, Herb-Robert, is universally distributed. Erodium, the Stork's-bill, has the 5 stamens which are opposite to the petals transformed into staminodes; *E. cicutarium* is common in waste places. Pelargonium, in many varieties, is a well-known garden-plant: the flowers are irregular and dorsiventral; the disc is absent, but the posterior sepal is provided with a glandular spur which adheres to the pedicel. The cocci of Erodium and Pelargonium are indehiscent, and are forced into the ground by the movement of the hygroscopic awn.

Order 2. Linaceæ. Disc generally a whorl of 10 small extrastaminal glands: formula $K5$, $C5$, $(\mid A \dagger 5+5)$, $G^{(\underline{5})}$: flowers actinomorphic, rarely all the whorls are tetramerous: stamens monadelphous at the base; the whorl of stamens opposite to the petals is replaced by staminodia: each loculus of the ovary contains two ovules, and is often divided into two by a more or less complete false dissepiment: seed usually contains endosperm: capsule septicidal. Herbs or shrubs; leaves simple, entire, with or without stipules.

Linum usitatissimum is the Flax: the strong bast-fibres are used in weaving linen; the seeds contain oil; the walls of the outer cells of the testa are mucilaginous. There are several British species of Linum. Radiola, the other British genus, has tetramerous flowers.

Order 3. Erythroxylaceæ. Flowers regular: petals five, with a ligular appendage: stamens ten, connate at the base by means of a disc and forming a tube: ovary 2–3-locular, with one suspended anatropous ovule in each loculus: seed with endosperm.

The wood of most of the species contain a red dye. The leaves of *Erythroxylon Coca* are used as a stimulant: they contain cocaïn.

Order 4. Oxalidaceæ. Disc present as small glands at the base of the antipetalous stamens, or of all of them: flowers actinomorphic; formula $K5$, $C5$, $(\mid A5+5)$, $G^{(\underline{5})}$; the antipetalous stamens are sometimes staminodial; those which are opposite to the sepals are the longest: ovules numerous; fruit a capsule, or more rarely a berry; seed containing endosperm. Herbs, with compound (ternate), generally exstipulate leaves.

Oxalis Acetosella, the Wood-Sorrel, is frequent in woods; it contains much potassium oxalate. The tuberous roots or underground stems of some American species, as *O. esculenta*, *crenata*, and *Deppei*, contain much mucilage, and are used as food. Some species (*e.g. O. gracilis*) show trimorphic heterostylism (p. 455): others (*e.g. O. Acetosella*), have cleistogamous flowers (p. 453). The leaves of Oxalis and Averrhoa show sleep-movements: those of Biophytum are sensitive to touch.

Order 5. Balsaminaceæ. Disc 0: flowers irregular, dorsiventral; formula $K5$, $C5$, $\mid A0+5$, $G^{(\underline{5})}$: the posterior sepal is spurred, and the two anterior are small or absent: the anterior petal is large: ovary 5-locular; ovules numerous; the fruit is loculicidally septifragal, the valves separate elastically and roll upwards, so that the seeds are projected to some distance; seed without endosperm. Herbs, with simple exstipulate leaves.

Impatiens Noli-me-tangere, the yellow Wild Balsam, occurs in damp and shady spots; the ripe fruit flies open with violence at a touch. *Impatiens Balsamina*, an Indian species, is cultivated.

Order 6. TROPÆOLACEÆ. Disc 0: flowers irregular, asymmetric (Fig. 328 *B*, p. 513); formula $K5$, $C5$, $A4+4$, $G^{\underline{(3)}}$: the posterior sepal is prolonged into a spur; the three anterior petals are clawed and ciliate: the two median stamens, one belonging to each whorl, are suppressed, so that there are eight instead of ten: one ovule in each of the three loculi of the ovary: seed without endosperm. Herbs, with exstipulate leaves; often petiole-climbers.

Tropæolum majus and *minus*, Indian Cress, often wrongly termed Nasturtium, are universally cultivated.

Order 7. ZYGOPHYLLACEÆ. Disc annular, fleshy: flowers actinomorphic, 5 or 4-merous. Herbs or shrubs with decussate, frequently paripinnate, stipulate leaves: seeds with endosperm.

Lignum Vitæ is the wood of *Guiacum officinale* (West Indies).

Order 8. RUTACEÆ. Disc usually annular: flowers usually actinomorphic and obdiplostemonous: gynæceum sometimes partially apocarpous, but the styles are usually connate: seed with or without endosperm. There are numerous oil-glands on the leaves and stems.

Sub-order 1. RUTEÆ. The placentæ project into the loculi of the ovary; each bears 3 or more ovules: fruit a loculicidal capsule: seed with endosperm.

Ruta graveolens, the Rue, has pentamerous terminal flowers, and tetramerous lateral flowers. *Dictamnus Fraxinella* has an irregular dorsiventral flower.

FIG. 415.—Diagram of the flower of Dictamnus.

Sub-order 2. DIOSMEÆ. Ovules 2 in each loculus: leaves simple: seed without endosperm.

Barosma, Agathosma, Empleurum.

Sub-order 3. ZANTHOXYLEÆ. Flowers usually diœcious and polygamous: endosperm usually present.

Zanthoxylum fraxineum, from North America, is a shrub which is sometimes cultivated.

Sub-order 4. TODDALIEÆ. Gynæceum syncarpous: fruit indehiscent, winged, dry or succulent: seed with endosperm.

Ptelea trifoliata is a North American shrub with white flowers.

Sub-order 5. AURANTIEÆ. Gynæceum syncarpous: calyx gamosepalous: seed without endosperm.

The genus Citrus has an indefinite number of bundles of connate stamens (polyadelphous) (Fig. 416 *A*), all belonging apparently to the antisepalous inner whorl: the carpels are usually more numerous than the petals, and during ripening they become filled with a succulent tissue derived from their walls; the various parts of the flower and the fruit (p. 532) contain much ethereal oil:

the leaf, which is typically pinnate, is reduced to its terminal leaflet which is articulated to the winged petiole (Fig. 32 *G*); the leaf is sometimes spinous.

Citrus medica is the Citron; *C. medica* var. *Limonum*, is the Lemon; *C. medica* var. *Limetta*, is the Lime; *Citrus Aurantium* var. *Bigaradia* (or *C. vulgaris*) is the Bitter or Seville Orange, and *C. Aurantium sinense* is the Sweet Orange; *Citrus nobilis* is the Mandarin Orange; and *Citrus decumana* is the Shaddock: all originally derived from tropical Asia.

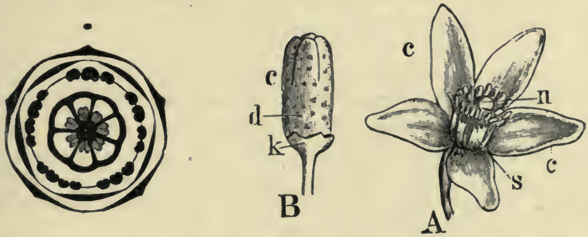

FIG. 416.—Flower and floral diagram of Citrus. *A* Open flower; *c* corolla; *s* the partially connate stamens; *n* the stigma. *B* Bud; *k* calyx; *c* corolla; *d* oil-glands.

Order 9. MELIACEÆ. Disc various: stamens 5-10, generally monadelphous; the filaments have stipulate appendages; carpels usually 5; no oil-glands, but simple sacs (p. 139).

Mahogany is the wood of *Swietenia Mahagoni* (America). The wood of species of Cedrela is often erroneously termed "cedar-wood": Guarea, Carapa, Melia, are other well-known genera.

Order 10. SIMARUBACEÆ. Disc conspicuous: flowers actinomorphic, sometimes diclinous: stamens usually 10, and then sometimes (*e.g.* Ailanthus) distinctly obdiplostemonous: gynæceum sometimes apocarpous: ovule usually solitary in each loculus: there are no oil-glands in the leaves, but the cortex and wood contain a bitter substance.

Ailanthus glandulosa, the Tree of Heaven, from China, is a tree with multijugate pinnate leaves and a winged indehiscent fruit; it is often cultivated.

Order 11. BURSERACEÆ. Disc usually annular: flowers actinomorphic: gynæceum syncarpous; ovary with two ovules in each loculus: there are resin-passages in the bast.

Boswellia serrata (East Africa) yields Olibanum, a gum-resin; *Commiphora Schimperi* and *abyssinica* yield the gum-resin Myrrh (Arabia and Abyssinia).

Cohort II. **Sapindales.** Flowers typically pentamerous and obdiplostemonous but with reduction in the andrœcium, actinomorphic or zygomorphic, sometimes monosporangiate: gynæceum oligomerous, usually syncarpous. Mostly trees.

Order 1. SAPINDACEÆ. Flowers usually irregular, obliquely zygomorphic or asymmetric, in that the two petals of one side are larger and of somewhat different form to the three others; of these, one, which lies in the plane of symmetry, is sometimes wanting: two or three of the antisepalous stamens are usually suppressed, so that the number is eight or seven; they are inserted within the disc: the ovary is trilocular; ovules two in each loculus: seed without endosperm.

Æsculus has opposite, palmately compound, exstipulate leaves; the flowers are in terminal scorpioid racemes; the fruit has a loculicidal dehiscence: *Æ. Hippocastanum* is the Horse-Chestnut, derived from Asia; *Æ. carnea*, *Æ. Pavia*, and other species are frequently cultivated. A great number of genera and species grow in warm climates; they have generally scattered pinnate leaves: often climbers with branch-tendrils. The fleshy fruit of *Sapindus Saponaria* makes a lather with water like soap.

FIG. 417.—Floral diagram of Æsculus: but the missing stamens should be represented as antisepalous.

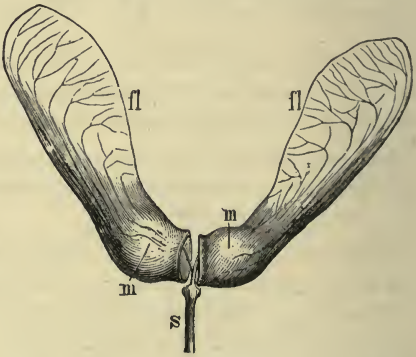

FIG. 418.—Fruit of *A. platanoides*, dividing into two mericarps *m*; *s* pedicel; *fl* wings (nat. size).

Order 2. ACERACEÆ. Flowers regular: stamens commonly eight, in consequence of the suppression of the two median ones, variously inserted: disc annular, rarely absent, extrastaminal or intrastaminal: ovary bilocular; ovules two in each loculus; when ripe the fruit splits into two one-seeded winged mericarps (samaras) (Fig. 418): leaves opposite, palmately lobed, sometimes compound, exstipulate: flowers in terminal racemes, sometimes in corymbs, with an apical flower: seed without endosperm.

The principal species of Acer, the Maple, are *A. Pseudoplatanus*, the Sycamore, having leaves with crenate margins, flowers in elongated pendulous racemes, blooming after the unfolding of the leaves, and parallel-winged fruits; *A. platanoides*, having leaves with serrate margins, flowers in short erect racemes blooming before the unfolding of the leaves, and fruits with widely diverging wings (even more than in Fig. 418); *A. campestre*, the common Maple, which is sometimes shrubby, with a trilobate leaf, short erect racemes of flowers which bloom after the unfolding of the leaves, and fruits with wings which are diametrically opposite. Some North American species are often cultivated, such as *A. rubrum*, with five stamens opposite to the sepals, and a rudimentary disc; *A. dasycarpum*, with the same number and position of the stamens, without any corolla, and having diœcious flowers; *A. Negundo*, with compound 3–5 foliolate leaves, and diœcious flowers like those of the preceding species. Sugar is prepared from the sap of *A. saccharinum* and *dasycarpum* especially.

Order 3. POLYGALACEÆ. Flowers irregular, dorsiventral; the two lateral sepals conspicuously large and known as "wings" (Fig. 419 k'): petals three, the two lateral being absent; the anterior petal is very large and carinate: stamens usually eight, forming a tube open posteriorly, to which the corolla, or at least the anterior petal, is adnate (Fig. 419*B*): disc rudimentary: carpels two, median, forming a bilocular ovary, each loculus containing a single suspended ovule: fruit usually a capsule. The flower somewhat resembles that of the Papilioneæ, but it must be borne in mind that here the two "alæ" or wings belong to the calyx.

FIG. 419.—Flower of *Polygala grandiflora*. *A* Seen from outside after the removal of the wing-sepal *k*. *B* Longitudinal section: *k* calyx; *k'* wing; *c* corolla; *s* tube of stamens. (After Sachs.)

The flower of the Polygalaceæ resembles that of the Aceraceæ in the suppression of two stamens in the plane of the two carpels.

Polygala vulgaris, *amara*, and others, the Milkworts, are herbs, woody at the base, occurring in woods and meadows.

Order 4. ANACARDIACEÆ. Flowers usually actinomorphic, and often diclinous: stamens usually inserted on the disc, but disc sometimes absent: gynæceum of but few carpels; sometimes one only is developed, the others being represented by two or more stigmata; each loculus of the ovary contains one anatropous ovule with dorsal raphe: resin-ducts present: seed without endosperm.

Various species are cultivated as ornamental plants. In Cotinus many of the flowers are abortive, and the hairy peduncles become much elongated. The genus Rhus includes the Sumachs; there are no antipetalous stamens: *R. Coriaria* (Southern Europe) is used in tanning. *Pistacia vera*, in Southern Europe, bears edible seeds (Pistachio-kernels); in the flowers of this genus the petals, and in the ♂ flower the stamens which are opposite to them, are suppressed.

FIG. 420.—Floral diagram of Rhus.

Cohort III. **Celastrales.** Flowers regular, frequently actinomorphic, 4–5-merous; only one whorl of stamens, which either alternates with or is opposite to the petals, is usually present: disc usually within, sometimes external to, the andrœcium: ovules usually erect: the seed nearly always contains endosperm. Trees or shrubs.

Order 1. CELASTRACEÆ. Formula, *K*n, *C*n, *A*n, *G* (n) or less, n=4 or 5: sepals imbricate: stamens and carpels inserted on a flattened disc: stamens alternate with the petals: usually two ovules in each loculus of the ovary: leaves scattered, entire, stipulate.

In the genus Euonymus, the Spindle-tree, the loculicidal capsule contains seeds invested by an orange-coloured arillode (p. 459); *E. europœa* occurs both cultivated and wild.

Order 2. STAPHYLEACEÆ. Flowers pentamerous: stamens alternate with the petals: disc intrastaminal: ovary generally trimerous and trilocular; ovules numerous: leaves decussate, pinnate, stipulate: seed with small endosperm.

Staphylea pinnata is grown in gardens.

Order 3. RHAMNACEÆ. Formula, *K*n, *C*n, | *A*n, $G^{\underline{(2\text{-}4)}}$; n=4 or 5: calyx usually gamosepalous, valvate: petals usually small and often hood-shaped (Fig. 421 *c*), enclosing the stamens which are opposite to them: flowers sometimes diclinous: usually a single ovule in each loculus of the ovary which is invested by a disc: leaves usually scattered, entire, stipulate: fruit a drupe or a capsule.

FIG. 421.—Flower of *Rhamnus Frangula* (mag.): *k* sepals connate at the base into a tube (*d*); *c* hood-shaped petals enclosing the stamens (*a*).

Rhamnus cathartica, the Buckthorn, has opposite leaves and thorny twigs: the berries of *R. infectoria*, in Southern Europe, yield a green or yellow dye; *R. Frangula* has scattered leaves; its wood produces a particularly light charcoal.

Order 4. Ampelidaceæ. Formula same as in Rhamnaceæ: sepals small; the corolla is often thrown off before it opens (Fig. 422 *A c*): a glandular disc between the andrœcium and the gynæceum: ovules one or two in each loculus: fruit baccate. Climbing plants, with stem-tendrils; leaves palmate, exstipulate or stipulate.

Vitis vinifera, the Grape-Vine, probably derived from the East, is cultivated in endless varieties; other species, such as *V. vulpina* and *Labrusca*, as also *Ampelopsis hederacea*, the Virginian Creeper, are also frequently cultivated. The tendrils of the Vine (Fig. 24 *A*) are branches bearing scaly leaves in the axils of which other branches arise: their peculiar position opposite to the foliage-leaves may be explained as follows: the ordinary shoots are sympodia, and each tendril is the terminal segment of a member of the sympodium; the following member is a shoot springing from the axil of the foliage-leaf which is opposite to the tendril. Every third leaf has no tendril opposite to it, that is to say, the members of the sympodium alternately bear one or two leaves. The inflorescences occupy the same positions as the tendrils. Each leaf has also a bud in its axil, which either remains undeveloped or gives rise to a dwarf-shoot: from the axil of the cataphyllary leaf of the dwarf-shoot an ordinary shoot is developed. In some species of Ampelopsis (*e.g. A. Veitchii* and *Roylei*) the tendrils attach themselves to flat surfaces by means of discoid suckers developed at their tips.

FIG. 422.—Flower of *Vitis vinifera*, and diagram. *A* At the moment of opening. *B* Open; *k* calyx; *c* corolla; *d* glands; *s* stamens; *f* ovary; *n* stigma (slightly mag.).

Order 5. Aquifoliaceæ. Disc wanting: one or two suspended ovules in each loculus of the usually tetramerous ovary: stamens free, or adnate to and alternate with the petals: petals often connate at the base: leaves scattered, exstipulate.

Ilex Aquifolium, the Holly, with its coriaceous, spinous, evergreen leaves, is common in plantations and woods: fruit a berry. The leaves known in commerce as Paraguay tea are derived from *I. paraguensis* in South America.

Order 6. Thymelæaceæ. Flowers more or less perigynous, with a disc; calyx and receptacle petaloid, with a four-lobed limb (Fig. 329 *D*); corolla often suppressed, or more or less rudimentary: stamens sometimes in two whorls, and then the four stamens opposite to the sepals are inserted higher on the tube of the calyx than the four which alternate with the sepals (Fig. 423): gynæceum usually monomerous; ovule suspended; fruit a berry: seed without endosperm.

Daphne Mezereon is common in woods; the usually 3-flowered inflorescences are borne in the axils of the foliage leaves of the previous year, and they bloom before the development of the leaves of the same year.

This order is frequently placed among the Monochlamydeæ, but this position is untenable in consequence of the presence of a corolla in some genera (*e.g.* Gnidia).

Order 7. ELÆAGNACEÆ. Flowers diclinous or polygamous, 4- or 2-merous; the corolla is suppressed: the stamens opposite to the sepals are sometimes wanting (Fig 424 *B*); a disc (Fig. 424 *A*, *d*) usually closes the receptacle: fruit an achene, surrounded by the receptacle or by the whole perianth: gynæceum monomerous: ovule basal: seed with small endosperm: the leaves are covered, especially on the under surface, with scaly hairs.

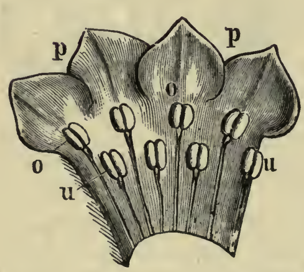

FIG. 423.—Calyx of the flower of *Daphne Mezereon* laid open (× 5): *o* the four superior, *u* the four inferior stamens, adnate to the calyx.

FIG. 424.—Flower of *Elæagnus fusca.* *A* In longitudinal section. *B* Floral diagram: *d* disc (mag.: after Sachs).

This order is also frequently placed among the Monochlamydeæ: but although no corolla is indicated, the order must be retained near the Thymelæaceæ.

Hippophaë rhamnoides, the Sea Buckthorn, is a shrub which is sometimes common on the banks of streams; the smaller branches mostly terminate in a thorn; the flowers are diœcious and dimerous; when the fruit is ripe the fleshy receptacle is of an orange colour. Elæagnus has tetramerous polygamous flowers (Fig. 424); it is commonly cultivated.

Cohort IV. **Euphorbiales.** Flowers monosporangiate, monœcious or diœcious; the perianth sometimes consists of calyx and corolla, sometimes it is simple, and occasionally it is absent: the ovary is usually trilocular, with one or two anatropous and generally suspended ovules in each loculus: the seed contains endosperm: the structure of the flowers is very various. The affinities of the cohort are not accurately known; but it can no longer be retained among the Monochlamydeæ.

Order 1. EUPHORBIACEÆ. The flower exhibits all possible degrees of reduction. The perianth may consist of calyx and corolla (*e.g.* some Phyllantheæ, such as Andrachne, Savia, Bridelia; some Crotoneæ, such as Chrozophora, Croton sub-gen. Eluteria, Jatropha, Cluytia, etc.): more commonly the corolla is suppressed, and in some cases (*e.g.* Euphorbia) the calyx also. The andrœcium varies from 1 to 8 stamens: thus in Euphorbia the ♂ flower consists of a single stamen, whilst in Ricinus the stamens are numerous and repeatedly branched (Fig. 333): they are sometimes isomerous with the perianth-leaves. The gynæceum is typically trimerous, but the carpels may be more numerous (5–20 in Hura) or fewer (1 in Eremocarpus): the syncarpous ovary has as many loculi as there are carpels: each loculus contains one or two (then collateral) suspended anatropous ovules, the micropyles of which are directed outwards; the micropyle is usually invested by a micropylar aril (see p. 459), often termed the caruncle, which is conspicuous on the seed. The fruit is usually dry and dehiscent, splitting septicidally into cocci. A disc is commonly present, and is frequently annular in the ♀ flowers: in the ♂ flowers the disc is usually extra-staminal.

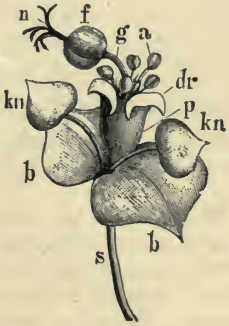

FIG. 425.—Part of an inflorescence of a Euphorbia: *b b* bracts, in the axils of which are the buds (*kn*): *p* is the involucre of the open cyathium; *dr* the glands; *a* the ♂ flowers; *g* the pedicel of the ♀ flower (*f*); *n* the stigmata (enlarged).

They are plants of various habit, from herbs to trees, some resembling species of Cactaceæ. Many of them possess laticiferous tissue (absent in Phyllantheæ and some Stenolobeæ), consisting either of laticiferous coenocytes (Euphorbieæ: see p. 142) or of laticiferous vessels (Crotoneæ): the latex is usually milky, and in this case the laticiferous tissue is more highly developed than when (as in Mercurialis) the latex is not milky.

The inflorescence requires special consideration: it is, generally speaking, of the mixed type, the earlier branchings being racemose whilst the final branchings are cymose: in the monœcious plants, as a rule, both kinds of flowers are borne in the same inflorescence, the ♀ flowers above, the ♂ flowers below.

In the family Euphorbieæ the general inflorescences are cymose umbels or dichasia, the branches of which terminate in what were formerly regarded as ambisporangiate flowers, but are really inflorescences, each one being termed a *cyathium*. The cyathium consists of a tubular involucre (Fig. 425 *p*), consisting of bracts, often brightly-coloured (*e.g.* Poinsettia), between the five lobes of which glandular appendages, often of a semilunar form, are situated (Fig. 425 *dr*). Within this involucre are numerous ♂ flowers in five groups, each of which consists of a single stamen (Fig. 425 *a*) and is terminal on a long pedicel, and one ♀ flower (Fig. 425 *g*), consisting of a trilocular ovary (Fig. 425 *f*), at the base of which an indication of a perianth may in some cases be detected. That the cyathium is an inflorescence and not a single flower is most clearly visible in the genus Anthostema, in which a perianth is distinctly developed round each stamen.

Of Euphorbia, the Spurge, most indigenous species are annual herbs, as *E. Peplus, exigua, platyphyllos* and *helioscopia* (the common Sun Spurge), whilst others are perennial (*E. amygdaloides*, and *Paralias*): some South European forms are small shrubs, as *E. dendroides* and *fruticosa*: in Africa and the Canary Islands the genus is represented by species which much resemble Cactaceæ in appearance; their stems are thick and cylindrical or angular or sometimes spherical, producing small leaves which usually soon fall off. In Mercurialis the flowers are apetalous; the ♂ flowers have a three-leaved perianth and numerous stamens; the ♀ flowers have a similar perianth and a bilocular ovary: *Mercurialis annua* and *perennis* (Dog's Mercury) are weeds, the first common in cultivated ground, the second in woods; their flowers are diœcious. Ricinus bears its monœcious apetalous flowers in a compound inflorescence, in which the ♂ flowers are placed below and the ♀ flowers above: the perianth is simple and five-lobed: *Ricinus communis* (the Castor-oil plant) is a native of Africa, now frequently cultivated; Castor-oil is obtained from its seeds. Croton-oil is obtained from the seeds of *Croton Tiglium*. Some species of Phyllanthus (Xylophylla) have phylloid branches which bear their small flowers in the axils of minute bristle-like leaves situated in indentations at the edge of the phylloclade. The root of *Manihot utilissima*, a South American plant, when ground, constitutes cassava, and it yields the starchy meal known in commerce as tapioca. From *Siphonia elastica*, a species growing in Central America, most of the caoutchouc is obtained.

Order 2. **Buxaceæ.** Disc wanting: flowers monœcious, in glomerules in which the terminal flower is usually ♀ and the lateral ones ♂; the latter flowers have a simple 4-leaved perianth and four superposed stamens (rarely numerous); the former have a trilocular ovary with two ovules in each loculus, the micropyle of the suspended ovule being directed inwards: fruit a capsule, with loculicidal dehiscence. For the most part shrubs.

Buxus sempervirens, the Box, is an evergreen shrub of Southern Europe; the wood is valuable.

Order 3. EMPETRACEÆ. Disc wanting: flowers diœcious, with three sepals, three petals, three stamens or a 6–9-locular ovary: ovules solitary, ascending: fruit drupaceous. They are shrubs resembling Heaths in appearance.

Empetrum nigrum, the Crakeberry, is a small shrub occurring in the north of Europe and in the Alps.

Order 4. CALLITRICHACEÆ. Aquatic plants, with decussate, linear or ovate leaves, in the axils of which stand the solitary diclinous flowers which are destitute of a perianth: the ♂ flowers consist of a single stamen; the ♀ of a bilocular, spuriously quadrilocular, ovary, with four suspended ovules, the micropyles of which are directed outwards.

Callitriche verna and other species, forming the section Eu-callitriche, are either partially submerged or they creep on muddy banks, and in them pollination takes place in the air: but in the section Pseudo-callitriche (of which *C. autumnalis* is the British representative) the plants are entirely submerged, and consequently pollination takes place under water (see p. 434).

This order has been associated with the Haloragidaceæ; but the general structure of the flower, especially the remarkable reduction which it presents, and the number and attachment of the ovules, seem rather to indicate affinity with the Euphorbiaceæ.

SERIES III. CALYCIFLORÆ.

Flowers epigynous or perigynous: calyx usually gamosepalous: stamens definite or indefinite: gynæceum syncarpous or apocarpous.

Cohort I. **Umbellales.** Flowers regular, sometimes actinomorphic, epigynous, with generally a single whorl of stamens opposite to the sepals: calyx inconspicuous: ovary bilocular, with one ovule in each loculus: a disc between the stamens and the styles: inflorescence usually umbellate: seed containing endosperm: leaves exstipulate.

Order 1. UMBELLIFERÆ. Flowers generally regular, but zygomorphic in consequence of oligomery in the gynæceum (p. 508): formula, $K5$, $C5$, $A5$, $G_{\overline{(2)}}$: the calyx is generally very small, often hardly visible, though sometimes well developed (*e.g.* Eryngium, Astrantia): the corolla consists of five rather small white or yellow petals; occasionally the outermost petals of the flowers at the circumference of the umbel are larger than the others, and the umbel is then termed *radiant*: stamens five; ovary inferior, bilocular: the base of the two styles is fleshy and thickened, forming an epigynous disc (Fig. 426 *A d*); one suspended ovule in each loculus of the ovary (Fig. 338 *E*): the fruit, when ripe, splits into two mericarps, each loculus of the ovary being permanently closed by a median septum (Fig. 427*a*; see p. 530). The structure of the pericarp is an important characteristic for the classification of the family. The fruit is commonly either oval in form, or compressed (Fig. 426 *B*), or nearly spherical (Fig. 426 *E*): its surface generally bears longitudinal ridges (*costæ* or *juga primaria*) enclosing vascular bundles, five generally on each mericarp; of these, two run along the margins (Fig. 426 *B*, *C*, *D*, *rr*), and the other three along the dorsal surface (Fig. 426 *B*, *C*, *D*, *r*). In the spaces between the ridges which form furrows, lie oil-ducts or receptacles

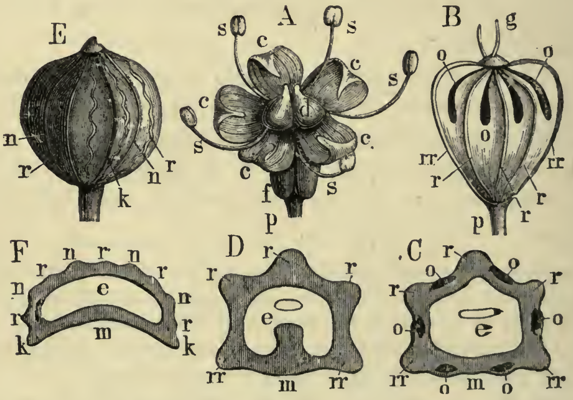

FIG. 426.—*A* Flower of Fœniculum (mag.): *f* ovary; *c* corolla; *s* stamens; *d* disc. B Fruit of Heracleum: *p* pedicel; *g* style; *r r r* ridges (costæ): *rr* marginal ridges; *o* oil-ducts (vittæ) (mag.). *C* Transverse section of mericarp of *Carum Carui* (*Orthospermeæ*): *m* surface that comes into contact with the other mericarp; *o* vittæ; *e* endosperm. *D* Transverse section of mericarp of Conium (*Campylospermeæ*). *E* Fruit of Coriandrum, (*Cœlospermeæ*): *k* margins of the surface along which the two mericarps are in contact; *r* ridges; *n* secondary ridges: **F** section of a mericarp. (Mag.)

(*vittæ*) (Fig. 426 *B*, *C*, *o*), and sometimes other secondary ridges, (*juga secundaria*) (Fig. 426, *E*, *F*, *n*), which do not enclose vascular bundles. The mericarp when ripe is filled by the seed, which consists of the abundant endosperm (Fig. 426 *C*, *D*, *F*, *e*) enclosing a small embryo. According to the form assumed by the endosperm, the following groups may be distinguished: the *Orthospermeæ*, in which the surface of the endosperm, which is directed towards the plane of junction of the two mericarps, is flat or convex, as in Carum (Fig. 426 *C*): the *Campylospermeæ*, in which the endosperm is concave towards the same plane, as in Conium (Fig. 426 *D*), and the *Cœlospermeæ*, in which the whole endosperm is curved, so that it is seen to be concave towards this plane both in longitudinal and in transverse section, as in Coriander (Fig. 426 *F*).

The flowers, with few exceptions (Hydrocotyle, Astrantia, Eryngium), are in compound umbels; in some few cases, as in Daucus, the umbel has a distinct terminal flower which is black in colour: an involucre and involucels are largely developed in some species, in others they are wholly wanting. The hollow stem bears large leaves with generally well-developed sheathing bases and much divided laminæ: rarely the leaves are simple, as in Hydrocotyle and Bupleurum.

Fig. 427.—Fruit of *Carum Carui*. *A* Ovary of the flower (*f*). *B* Ripe Fruit. The two carpels have separated so as to form two mericarps (*m*). Part of the septum constitutes the carpophore (*a*).

The British genera are arranged as follows:—

Sub-order I. Orthospermeæ.

A. Umbels simple.

Tribe 1. *Hydrocotyleæ.* Fruit laterally compressed. The genus Hydrocotyle consists of marsh-plants with peltate leaves (Fig. 31).

Tribe 2. *Saniculeæ.* Fruit nearly cylindrical. This group includes the genera Astrantia, Eryngium, and Sanicula.

B. Umbels compound.

Tribe 3. *Ammineæ.* Fruit without secondary ridges, laterally compressed: Ammi, Bupleurum, Petroselinum, Apium, Ægopodium, Carum (Figs. 426 *C*, and 427), Cicuta, Sium, Pimpinella, Trinia, Conopodium, Sison.

Tribe 4. *Seselineæ.* Secondary ridges absent, or if present (Siler) not so prominent as the primary: fruit not compressed: Æthusa, Fœniculum, Œnanthe, Seseli. Meum, Ligusticum, Silaus, Crithmum, Siler.

Tribe 5. *Angeliceæ.* Fruit without secondary ridges, dorsally compressed, the lateral primary ridges winged, the wings of the two mericarps divergent; Angelica, Archangelica.

Tribe 6. *Peucedaneæ.* Fruit without secondary ridges, dorsally compressed, the lateral primary ridges winged, the wings of the two mericarps apposed: Peucedanum (incl. Imperatoria), Pastinaca, Heracleum, Tordylium.

Tribe 7. *Daucineæ.* The secondary ridges are spinous: Daucus.

Sub-order II. CAMPYLOSPERMEÆ.

Tribe 8. *Caucalineæ.* Secondary ridges spinous: Caucalis (incl. Torilis).

Tribe 9. *Smyrnieæ.* Fruit without secondary ridges: Anthriscus, Myrrhis, Conium (Fig. 426 *D*), Smyrnium, Physospermum.

Sub-order III. CŒLOSPERMEÆ.

Tribe 10. *Scandiceæ.* Fruit sub-globose, without secondary ridges: Scandix, Chærophyllum, Echinophora.

Tribe 11. *Coriandreæ.* Fruit spherical; secondary ridges more prominent than the wavy primary ridges: Coriandrum (Fig. 426 *E*, *F*).

Anthriscus silvestris, the Cow-Parsley; *Carum Carui*, the Caraway; *Heracleum Sphondylium*, the Cow-Parsnip; *Ægopodium Podagraria*, the Gout-Weed; *Pastinaca sativa*, the Wild Parsnip, are common in meadows and woods: Crithmum, the Samphire, grows on rocks by the sea: Echinophora, the Prickly Samphire, growing on sandy sea-shores, has been exterminated in Britain. The following are cultivated: *Apium graveolens*, Celery; *Petroselinum sativum*, Parsley; *Daucus Carota*, the Carrot; *Pastinaca oleracea*, the Parsnip; *Anthriscus Cerefolium*, the Chervil. The following are poisonous: *Conium maculatum*, the Hemlock; *Cicuta virosa*, the Water-Hemlock; *Æthusa Cynapium*, Fool's-Parsley.

Order 2. ARALIACEÆ. Flowers generally pentamerous; stamens sometimes more numerous; carpels more or less numerous: fruit, a berry or a drupe. Shrubs, sometimes root-climbers, with scattered palmate leaves.

Hedera Helix, the Ivy, does not blossom till it is some years old: the umbels are borne on erect branches, the leaves of which are entire. *Fatsia papyrifera* is used in Japan for making a kind of paper known as rice-paper; it is made from the pith.

Order 3. CORNACEÆ. Flowers tetramerous, isobilateral (see p. 508), with a usually dimerous bilocular ovary: fruit usually a drupe. Shrubs with woody stems and entire opposite leaves.

Cornus mas, the Cornel, has yellow flowers which bloom before the unfolding of the leaves, and a red fruit: *C. sanguinea* and *suecica* are common shrubs: *Aucuba japonica* has diœcious flowers, and a monomerous baccate fruit.

Cohort II. **Passiflorales.** Flowers frequently monosporangiate, regular; epigynous, perigynous or hypogynous; pentamerous: stamens in one or two whorls, or indefinite: gynæceum syncarpous; ovary usually trimerous and unilocular; ovules numerous, on parietal placentæ.

Order 1. PASSIFLORACEÆ. Flowers pentamerous, perigynous, sometimes diœcious; between corolla and andrœcium there is a so-called corona consisting of a number of filamentous appendages, probably representing a disc (see p. 527): the gynæceum frequently, and sometimes also the andrœcium, is elevated upon an elongation of the axis (gynophore, or gonophore, p. 495): stamens five, often monadelphous, opposite to the sepals: ovary unilocular with three parietal placentæ: leaves palmate. Climbing plants, with tendrils, each tendril being a lateral axillary branch, and frequently the main axis of an inflorescence.

Several species of Passiflora, the Passion-Flower, from tropical America, are cultivated.

Order 2. PAPAYACEÆ. Flowers diclinous, hypogynous: stamens in two whorls: ovary usually unilocular with five parietal placentæ.

Carica Papaya, the Papaw, is cultivated in the tropics on account of its edible fruit: its latex is rich in proteolytic ferment (papain).

Order 3. BEGONIACEÆ. Affinity doubtful. Flowers diclinous; perianth rarely heterochlamydeous: the ♂ flowers have two dimerous petaloid perianth-whorls, and indefinite stamens crowded together: the ♀ flowers are epigynous; the perianth consists of five petaloid leaves; the ovary is usually trilocular, with numerous anatropous ovules borne on axile placentæ: fruit a capsule: leaves often very large, usually oblique: inflorescence cymose, the ♂ flowers being terminal on the first branches, the ♀ terminal on the last.

Many species of Begonia, derived from the tropics, are cultivated as ornamental plants.

Order 4. CUCURBITACEÆ. Flowers diclinous or polygamous, often irregular: corolla of five petals, often gamopetalous: stamens epipetalous, five, but they frequently cohere, either in pairs, so that there appear to be but three (Fig. 428, diagram), or all completely into a single continuous ring (Cyclanthera); the anthers are commonly long and sinuous: ovary inferior, unilocular, becoming spuriously multilocular, with one or (more often) many ovules; it is, however, often described as multilocular (usually 3) with projecting axile placentæ: fruit baccate, a pepo or a succulent berry, often of great size, with a relatively thick and solid pericarp: seed without endosperm. Herbs with scattered leaves, mostly climbers, with tendrils growing by the side of the leaves.

There is considerable difference of opinion as to the morphological nature of the tendril in this order, but it appears to be essentially a leaf, in fact the first leaf of the flowering-shoot which arises in the axil of the related foliage-leaf: the vegetative branch, which is always developed by the side of the flowering-shoot, seems to spring from the axil of the tendril. The tendril often bears a number of branches at its distal end, but, whether simple or branched, its structure shows that the proximal portion corresponds in structure to a petiole, whilst the distal irritable portion (including the branches) has a bilateral structure which suggests correspondence with a lamina.

Cucurbita Pepo is the Pumpkin: the genus Cucumis has free stamens; *Cucumis sativa* is the Cucumber, and *Cucumis Melo* is the Melon: *Citrullus vulgaris* is the Water Melon. The genus Bryonia has a small white corolla; the loculi of the ovary are 2-seeded, and the fruit is a succulent berry; *B. dioica* is common in shrubberies and hedges.

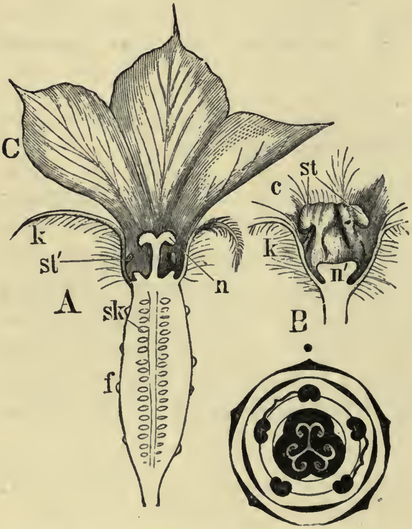

FIG. 428.—*A* Longitudinal section of ♀ flower of Cucumis: *f* ovary; *sk* ovules; *k* calyx; *C* corolla; *n* stigma; *st′* rudimentary stamens. *B* Longitudinal section of ♂ flower; *st* stamens; *n′* rudimentary ovary; the corolla (*c*) is not all shown (somewhat mag.). Floral diagram of Cucurbita.

Order 5. CACTACEÆ. Flowers acyclic, epigynous, with numerous sepals, petals, and stamens, which gradually pass into each other: ovary unilocular, with three or more parietal placentæ: ovules horizontal; endosperm little or none: stems of the most various forms: leaves usually represented by tufts of spines. They are indigenous to the dry districts of tropical and subtropical America, but many have been introduced into the eastern hemisphere: however, a species of the genus Rhipsalis (*R. Cassytha*) is indigenous to South Africa and Ceylon.

The Cactaceæ are typically xerophilous plants: in consequence of the great reduction of the foliage-leaves, their transpiration is comparatively slight, and the succulent stems serve to store relatively large quantities of water. They are protected from being eaten, by the development of numerous spines.

Mamillaria has a spherical or cylindrical stem on which tubercules, arranged spirally and bearing spines, represent the leaves. Echinopsis and Echinocactus have angular ridges on which the tufts of spines grow. Cereus has an angular, columnar, elongated stem. Phyllocactus and Rhipsalis have compressed leaf-like stems. Opuntia and Nopalea have flattened stems composed of a succession of flattened ovate shoots. The Cochineal insect lives on *Nopalea coccinellifera.*

Cohort III. **Myrtales.** Flowers usually actinomorphic, eucyclic, epigynous or perigynous, with usually two whorls of stamens, typically obdiplostemonous: gynæceum syncarpous, with usually a single style: leaves usually opposite.

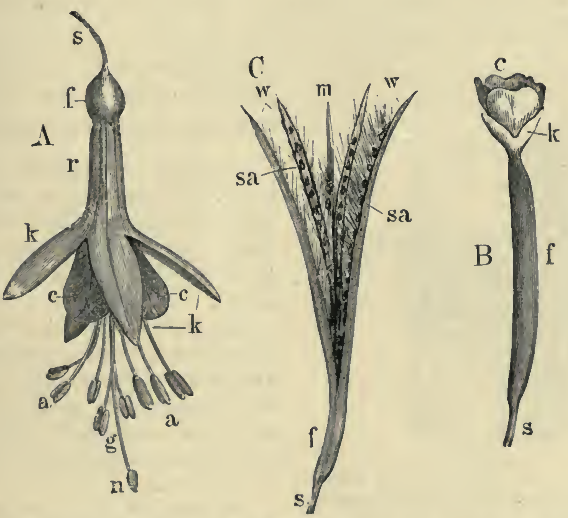

FIG. 429.—*A* Flower of Fuchsia: *s* pedicel; *f* inferior ovary; *k* sepals, connate at the base, forming a tube (*r*); *a* stamens; *g* style; *n* stigma. *B* Flower of *Epilobium hirsutum* (letters as before). *C* Fruit of Epilobium after dehiscence; *w* outer wall; *m* columella formed by the septa; *sa* seed with tufts of hairs (nat. size).

Order 1. ONAGRACEÆ. Flowers usually tetramerous throughout, generally epigynous: antipetalous stamens sometimes suppressed: ovary multilocular, with generally numerous ovules on axile placentæ: fruit a berry or a capsule; seed without endosperm. Calyx often petaloid, forming a long tube (Fig. 429 *A*, *r*).

Œnothera biennis, the Evening Primrose, occurs on river banks; the seed has not a tuft of hairs, and the flowers are yellow. Epilobium is the Willow Herb, of which many species are common; *E. angustifolium, hirsutum*, and *montanum* occur in fields, hedges, and ditches; the seeds have a tuft of long hairs; flowers red; fruit a septifragal capsule. *Circæa lutetiana* (Enchanter's Nightshade) has dimerous flowers $K2$, $C2$, $A2$, $G_{(2)}$ (Fig. 323 *B*); common in damp and shady spots. *Isnardia palustris* has no corolla; its fruit is a septicidal capsule. Fuchsia (Figs. 429 *A*, 323 *A*), many species of which are cultivated as ornamental plants, is a native of South America; fruit a berry.

Trapa natans, the Water-Chestnut, a not very common water-plant of Central Europe, has a stem bearing a rosette of leaves which float on the surface of the water; in the axils of these leaves the flowers are borne singly: their formula is $K4$, $C4$, $A4$, $G^{\underline{(2)}}$, and they are perigynous: the fruit is indehiscent, and the sepals remain adherent to it in the form of four horns: it contains two seeds.

Order 2. HALORAGIDACEÆ. Flower sometimes monosporangiate, epigynous, usually tetramerous throughout; stamens often in two whorls, and then obdiplostemonous: sometimes the corolla or the whorl of stamens opposite to the petals is wanting: ovary 1–4-merous, with a single suspended ovule in each loculus; seed containing endosperm.

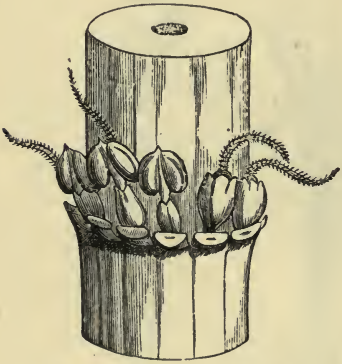

FIG. 430.—Part of a flowering stem of *Hippuris vulgaris*. The leaves are cut away. (After Sachs.)

Myriophyllum verticillatum and *spicatum*, the Water-Milfoils, are aquatic plants with finely divided leaves and small, generally diclinous, flowers borne above the water in terminal spikes.

The genus Gunnera includes land-plants with large leaves: the flower is dimerous, but is frequently reduced by the suppression of the corolla, or of one of the series of sporophylls (diclinous): the dimerous ovary produces but a single ovule.

The genus Hippuris consists of the single (British) species *H. vulgaris* the Mare's-tail. It is an aquatic plant, bearing its very much reduced flowers singly in the axils of the whorled leaves: there is no corolla, and the calyx is rudimentary: there is a single epigynous stamen, and a monomerous ovary containing a single suspended anatropous ovule.

Order 3. LYTHRACEÆ. Flowers perigynous, with usually both whorls of stamens: formula $Kn, Cn, \mid An + n, G^{\underline{(2-6)}}$, where $n = 3—16$: ovary free in the hollow receptacle: an epicalyx formed by connate stipules is often present: seed without endosperm.

Lythrum Salicaria, the Loosestrife, occurs in bogs and ditches: flower usually pentamerous or hexamerous: the stamens of the two whorls are unequal in length, and the length of the style also varies; three forms of flowers are thus produced (trimorphism; see p. 455): the other British genus is Peplis;

P. Portula is the Water-Purslane; it has usually hexamerous flowers and an indehiscent fruit: gynæceum dimerous in both genera. Several species of Cuphea, having a dorsiventral flower, with a posteriorly spurred calyx-tube, from Mexico, are cultivated.

Order 4. MYRTACEÆ. Flowers 4- or 5-merous, epigynous: stamens often very numerous, free, or connate in usually antipetalous bundles (Fig. 431); sometimes few and obdiplostemonous: ovary 1–∞-locular; seeds 1–∞ in each loculus, without endosperm: placentation and fruit various: leaves usually opposite, dotted with oil-glands. Shrubs or trees.

Tribe 1. *Myrteæ*. Fruit a berry or a drupe; stamens indefinite.

Myrtus communis is the Myrtle of Southern Europe; the genus Eugenia includes a number of ornamental shrubs, among which is *E.* (*Jambosa*) *Caryophyllus*, the buds and flowers of which yield the spice known as cloves (Fig. 432).

Tribe 2. *Leptospermeæ*. Fruit a capsule, dehiscing loculicidally from above downwards: stamens generally indefinite, frequently in bundles which are opposite either to the sepals or to the petals (Fig. 431).

FIG. 431.—Longitudinal section of the flower of Calothamnus: *f* ovary; *s* calyx; *p* corolla; *st* antipetalous bundle of stamens; *g* style. (After Sachs.)

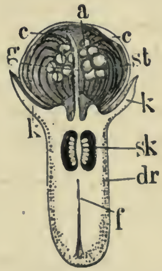

FIG. 432.—Flower-bud of *Jambosa Caryophyllus*, the Clove, in longitudinal section; *f* the inferior ovary, with the oil-glands (*dr*); *sk* the ovules; *k* calyx; *c* corolla; *st* stamens; *a* anthers; *g* style (enlarged).

Callistemon, Melaleuca, Metrosideros, Calothamnus, and others, are ornamental plants: *Eucalyptus Globulus*, from Australia, is much planted in marshy districts, which it tends to dry up by its active transpiration.

Tribe 3. *Chamælaucieæ*. Stamens often definite and obdiplostemonous: ovary unilocular: fruit usually one-seeded and indehiscent.

Tribe 4. *Lecythideæ*. Fruit large, woody, dehiscing with a lid, or indehiscent; leaves scattered, without oil-glands; stamens indefinite. This tribe is sometimes regarded as a distinct order, LECYTHIDACEÆ.

Bertholletia excelsa grows in tropical America; its seeds are known as Brazil nuts.

Tribe 5. *Granateæ.* Fruit resembling a pome; leaves opposite, without oil-glands. This tribe is sometimes regarded as a distinct order, PUNICACEÆ.

Punica Granatum, the Pomegranate, grows in Southern Europe; flowers 5–8-merous; receptacle petaloid; stamens indefinite; in the ovary there are two whorls of loculi, an external superior of which the loculi are as numerous as and are opposite to the petals, and an internal inferior consisting of three loculi.

Order 5. RHIZOPHORACEÆ. Tropical trees with aerial roots, known as Mangroves: the seed germinates in the fruit whilst it is still attached to the tree; when the projecting radicle has attained a length of one or two feet, either the whole fruit drops off, or only the radicle (incl. hypocotyl); in either case the pointed free end of the radicle sticks firmly in the mud on which the Mangroves grow.

The principal genera are Rhizophora, Bruguiera, Carallia.

Cohort IV. **Rosales.** Flowers actinomorphic or zygomorphic, usually ambisporangiate and perigynous: stamens rarely fewer in number than the petals or equal to them, generally indefinite in numerous whorls: gynæceum more or less completely apocarpous: ovules anatropous, suspended or erect: seed generally without endosperm.

Order 1. ROSACEÆ. Flowers actinomorphic, rarely zygomorphic, perigynous: gynæceum generally apocarpous; carpels 1–∞; ovules 1 or few, anatropous: fruit various; seed generally without endosperm: leaves scattered, stipulate; the odd sepal is posterior.

Tribe 1. *Roseæ.* Carpels numerous, attached to the base and sides of the hollow receptacle, which is narrow above (Fig. 433 *C*); each contains a single suspended ovule; when ripe, they are achenes enclosed in the fleshy receptacle: the sepals are frequently persistent at the top of it. Shrubs with imparipinnate leaves; the stipules are adnate to the petiole (see Fig. 316).

Many species of Rosa, the Rose, are wild, such as *R. arvensis*, *canina*, and *rubiginosa* (Sweet-Briar or Eglantine); and many others are cultivated, as *R. centifolia*, *damascena*, *indica*, *gallica*, etc.

Tribe 2. *Spiræeæ.* Carpels usually 5, each containing two or more suspended ovules; they are inserted upon the floor of the flat open receptacle, and become follicles; the calyx is persistent till the fruit is ripe.

Spiræa Ulmaria, Meadow-sweet, and *S. Filipendula*, Dropwort, occur in woods, meadows, etc.; *Sp. sorbifolia*, *media*, *ulmifolia*, and other species, *Kerria japonica*, and Rhodotypus (with drupes), are ornamental shrubs.

Tribe 3. *Pruneæ.* The single carpel, containing two suspended ovules, is inserted on the floor of the receptacle (Figs. 433 *A* and 434 *A*); the receptacle and the calyx fall off when the fruit is ripe: stamens usually in three whorls of 5 or 10; fruit a drupe (Fig. 344); only one seed is usually present.

Prunus is the principal genus of the tribe. In the sub-genus Amygdalus the fruit has a furrowed coriaceous endocarp; *Prunus Amygdalus* (*A. communis*), the Almond-tree, and *nana*, are trees of Southern Europe; *P. Persica* is the Peach: in the sub-genus Prunophora, the fruit has a smooth stony endocarp; *P. communis* (*spinosa*) is the Sloe or Blackthorn; *P. Armeniaca* is the Apricot *P. domestica* is the Wild Plum, it has an ovoid fruit and glabrous shoots; *P. insititia* is the Bullace, it has a globoid fruit and hirsute shoots: in the sub-genus Cerasus, *P. Cerasus*, the Dwarf or Morello Cherry, has foliage-leaves at the base of its umbellate inflorescences; *P. Avium*, the Wild Cherry or Gean, has only scales at the base of its inflorescences: in the sub-genus Laurocerasus, *P. Mahaleb*, the Damson, has fragrant bark; *P. Padus*, the Bird-Cherry, has elongated racemose inflorescences; *P. Laurocerasus*, the Cherry-Laurel, has evergreen leaves which somewhat resemble those of the true Laurel; *P. lusitanica* is the Portugal Laurel.

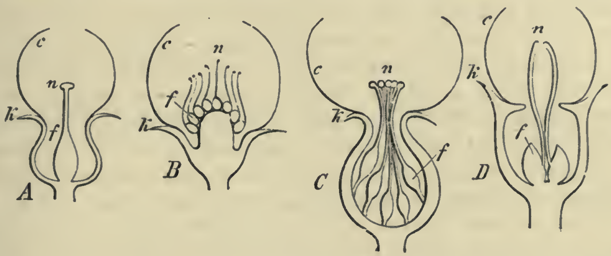

FIG. 433.—Diagrammatic longitudinal sections of Rosaceous flowers. *A* Pruneæ. *B* Potentilleæ. *C* Roseæ. *D* Pomeæ: *k* calyx; *c* corolla; *f* ovaries; *n* stigmata.

Tribe 4. *Poterieæ.* Flowers often monosporangiate: corolla often absent: ovaries few, often but one, monomerous, enclosed in the cavity of the receptacle which hardens as the seed ripens: ovules solitary, suspended.

The genus Alchemilla has tetramerous flowers destitute of a corolla, the stamens (4 or fewer) alternate with the sepals; an epicalyx is present: *A. vulgaris*, the Lady's Mantle, and *A. arvensis*, are common. In the genus Poterium, the flowers of the sub-genus Sanguisorba (*P. officinale*, the great Burnet), have no corolla, the four stamens are opposite the sepals, and they have no epicalyx: the flowers of the sub-genus Poterium (*P. Sanguisorba*, the Salad Burnet), resemble those of the preceding, but the stamens are indefinite, and they are polygamous. The flower of Agrimonia is pentamerous; it has a corolla and indefinite stamens; the outer surface of the receptacle is beset with bristles.

Tribe 5. *Potentilleæ.* The ovaries, which are numerous, are inserted upon a prolongation of the axis into the cavity of the receptacle (Figs. 433 *B* and 434 *B*); each usually contains one ovule. The calyx is often

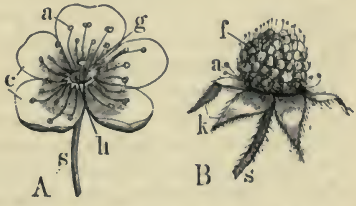

FIG. 434.—*A* Flower of the Cherry: *s* peduncle; *c* corolla; *a* stamens; *g* style, projecting out of the cavity of the receptacle. *B* Fruit of the Blackberry, *Rubus fruticosus*: *h* calyx; *f* fleshy ovaries.

surrounded by an epicalyx formed by the connate stipules of the sepals (Fig. 330 *C*). The stamens are usually indefinite, each whorl consisting of as many or twice as many stamens as there are petals. These flowers are distinguished from those of the Ranunculaceæ, which they somewhat resemble, by the whorled arrangement of the stamens and by the presence of the hollow receptacle; for in Ranunculaceous flowers the stamens are arranged spirally and the sepals are quite free.

Of the genus Potentilla, the Cinquefoil, which has dry fruits and a dry receptacle, many species are common, such as *P. anserina*, the Silver-weed, *reptans*, *Tormentilla*, and others: the sub genus Sibbaldia includes the species *P. procumbens*, which is found on Scottish mountains: the sub-genus Comarum includes the species *P. Comarum*, the Marsh Cinquefoil. Fragaria is the Strawberry; the receptacle becomes succulent as the fruit ripens and bears the small achenes on its surface; *F. vesca* and *elatior* are found in woods; *F. virginiana* and other North American species are cultivated. In the genus Rubus there is no epicalyx, the ovary contains two ovules, and the fruits are succulent (drupels); *Rubus Idæus* is the Raspberry; its fruits separate from the dry receptacle when they are ripe: in *R. fruticosus*, the Blackberry, and *R. cæsius*, the Dewberry, the upper part of the receptacle separates together with the fruits when ripe. *Dryas octopetala*, the Mountain Avens (without epicalyx) is a procumbent alpine shrub with an oval long-tailed fruit (resembling that of *Clematis Vitalba*). An epicalyx is present in most species of Geum: *Geum urbanum* and *rivale* (Avens) occur in woods and damp fields; the long style is hooked.

Tribe 6. *Pomeæ*. Ovaries five or fewer, contained in the cavity of the receptacle, connate, and adnate to the wall of the receptacle (Fig. 433 *D*). The spurious fruit is surmounted by the calyx. The individual fruits either become hard and are like small drupes imbedded in the fleshy receptacle, or they have only a thin wall, so that they are more like capsules and seem to be loculi of the whole fruit, as in the apple for instance, where the succulent portion is derived from the receptacle, and the core consists of the fruits enclosing the seeds. which are basal, generally two in each carpel. Stamens indefinite: no epicalyx, Shrubs or trees with deciduous stipules.

I. With stony fruits.

In the genus Cotoneaster, the fruits project above the receptacle: in Cratægus, the Hawthorn, they are completely enclosed; *C Oxyacantha*, the May, and its var. *monogyna*, the common White Thorn, are common; other species from the East and from North America are cultivated: Mespilus, the Medlar, has a large fruit which is surmounted by the five large sepals.

II. With coriaceous fruits.

The genus Cydonia, the Quince, has numerous ovules on the ventral suture of each carpel; the outer layers of cells of the testa are mucilaginous. The genus Pyrus has two basal ovules: *P. communis* and others are the Pear-trees; the loculi of the spurious fruit, seen in transverse section, are *rounded* towards the exterior; the fruit is not hollowed at the base: the sub-genus Malus includes *P. Malus* and others, the Apple-trees; the fruit is hollowed at the base, and the loculi, seen in transverse section, are *pointed* towards the exterior: the sub-genus Sorbus resembles the preceding, but has pinnatifid leaves; it includes *P. Aucuparia*, the Mountain Ash or Rowan-tree, as also *P. domestica*, the true Service-Tree, and *P. torminalis*, the Wild Service-Tree: the sub-genus Aria, includes *P. Aria*, the White Beam. The genus Amelanchier includes the European *A. vulgaris*, and *A. canadensis*, the June Berry. The genera Raphiolepis and Photinia (incl. Eriobotrya, the Loquat), include well-known cultivated flowering shrubs.

There are two other tribes of exotic Rosaceæ, the Quillaieæ, and the Chrysobalaneæ, concerning which it is impossible to go into detail; in the latter the gynæceum, which is monomerous as in the Pruneæ, is peculiar in that the style is gynobasic; and in some of the genera (Hirtellinæ), the flower is irregular and zygomorphic.

Order 2. LEGUMINOSÆ. Flowers usually dorsiventral, perigynous, pentamerous, with calyx and corolla: stamens ten or more: ovary of a single anterior carpel; ovules borne on the ventral suture: fruit a legume or a lomentum: flowers always lateral: leaves nearly always compound.

The Leguminosæ, more particularly the Papilioneæ, are remarkable physiologically by the presence of tubercles on their roots, caused by the attack of a Fungus, and by their extraordinary faculty of flourishing in soils poor in combined nitrogen: these two facts are undoubtedly correlated, but the exact nature of the correlation is still a matter of discussion (see Part IV.).

Sub-order 1. PAPILIONEÆ. Flowers dorsiventral, papilionaceous (Fig. 327 *A*). The five sepals, the odd one being anterior, are usually connate, forming a tube above the insertion of the corolla and the andrœcium: the five lobes are usually unequal and sometimes form two lips, the lower of three and the upper of two teeth: petals five, alternate with the sepals, imbricate so that the anterior petals are overlapped by those behind them; the posterior petal is much enlarged, and is called the *vexillum* (Fig. 435 *A fa*); the two lateral petals, which are much smaller, are termed the *alæ* (Fig 435 *A*, *fl*); the two anterior petals are connate or sometimes simply apposed, and form a hollow boat-shaped body, the keel, or *carina* (Fig. 435 *A*, *s*). In a few cases the corolla is entirely or partially suppressed; thus in Amorpha, only the vexillum is present. The ten stamens belong to a single whorl, with direct diplostemony; they are either connate and monadelphous, forming a tube, or the posterior stamen may be free, so that the tube consists of nine stamens, and is incomplete posteriorly (Fig. 435 *B*), in which case the andrœcium is diadelphous (9–1); rarely the stamens are all free; they mostly curve upwards, and diminish in length from in front backwards. The ovary, enclosed by the staminal tube, consists of a solitary anterior carpel; it is often divided into chambers by a spurious longitudinal septum, or

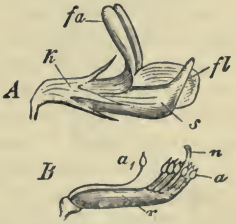

FIG. 435.—Flower of *Lotus corniculatus* (somewhat mag.). *A* With one ala removed; k calyx; *fa* vexillum; *fl* ala; s carina. *B* With the corolla removed; *r* tube formed by the nine stamens; *a*, the free stamen; *a* anther; *n* stigma.

by transverse septa into several chambers. The fruit is usually a legume or a lomentum (Fig. 312 *A*), rarely one-seeded and indehiscent : the seed frequently contains scanty endosperm. The flowers are solitary and axillary, or in racemes. The leaves are only rarely entire, usually palmately or pinnately compound, with often large stipules (Fig. 28 *C*), which are sometimes spines (Robinia).

Tribe 1. *Sophoreæ.* Stamens all free: leaves usually compound pinnate; trees or shrubs. Species of Sophora, Cladrastis, and Virgilia, are cultivated.

Tribe 2. *Podalyrieæ.* Stamens all free : leaves usually simple or ternate: shrubs or herbs. Species of Baptisia and Thermopsis are cultivated as herbaceous plants in gardens.

Tribe 3. *Genisteæ.* Stamens usually monadelphous: leaves simple or compound ternate.

In Ulex, the Whin, Gorse or Furze, Genista the Green-weed, Cytisus (Sarothamnus) the Broom, and Lupinus, the stamens are monadelphous; in Genista the leaves are simple; in Cytisus the leaves are ternate; in Ulex the leaves are ternate in seedlings, but in mature plants they are scaly or spinous; in Lupinus the leaves are palmately compound. *Cytisus Laburnum* is a well-known flowering tree.

Tribe 4. *Trifolieæ.* The posterior stamen is usually free; leaves ternate, and leaflets with serrate margins.

In Medicago (Medick), Melilotus, and Trifolium, the stamens are diadelphous: in Ononis, the Rest-harrow, they are monadelphous. Trifolium is the Clover: the stamens are partially adnate to the corolla; the withered corolla persists and encloses the small legume : flowers in capitula; *T. pratense*, the Red Clover, *T. repens*, the White Clover, and *T. hybridum*, the Alsike Clover, which are common in meadows, and *T. incarnatum*, from the East, are cultivated. Medicago has usually a spirally-wound legume, and a deciduous corolla; *M. falcata* and *lupulina* are common; *M. sativa*, Lucerne, is cultivated. Melilotus (Melilot) has a globular legume; *M. alba* and *altissima* are common on the banks of streams. Trigonella is the Fenugreek.

Tribe 5. *Loteæ.* Stamens diadelphous, the posterior stamen being free: leaves pinnate; leaflets sessile, entire.

Lotus corniculatus, the Bird's-foot Trefoil, with a beaked carina and nearly straight legume, is common in meadows. In Anthyllis, the Kidney-Vetch, the stamens are monadelphous at first, the posterior stamen becoming more or less separate: *Anthyllis Vulneraria*, Ladies' Fingers or Woundwort, is common in dry pastures.

Tribe 6. *Galegeæ.* Stamens diadelphous : leaves multijugate imparipinnate; leaflets stalked.

Indigofera tinctoria, in the East Indies, produces Indigo. Glycyrrhiza is the Liquorice. Colutea, the Bladder Senna, has an inflated fruit: *C. arborescens* and various species of Caragana are cultivated as ornamental plants. *Robinia Pseudacacia*, the false Acacia, is a native of North America, but it has become naturalized. *Amorpha fruticosa* is a common shrub from North America. Astragalus has a legume with a spurious longitudinal dissepiment: very many species of it occur, especially in the East.

Tribe 7. *Hedysareæ.* Leaves imparipinnate; stamens diadelphous: fruit a lomentum, with transverse septa, dividing into segments. Cotyledons leafy, epigæal.

Hippocrepis, the Horse-shoe Vetch, and Coronilla are common in meadows; *Onobrychis sativa*, the Sainfoin, is cultivated. *Arachis hypogæa*, the Earth-Almond or Ground-Nut of tropical America, ripens its fruits in the earth. *Desmodium gyrans*, the Telegraph-plant, has motile leaflets.

Tribe 8. *Vicieæ.* Stamens diadelphous: legume unilocular; cotyledons hypogean; leaves paripinnate and usually cirrhose (see Fig. 28 *C*).

Vicia sativa, the Vetch, and *V. Faba*, the Bean, are cultivated: other species occur wild. *Pisum sativum* and *arvense*, the Pea, are cultivated. *Lens esculenta*, the Lentil, belongs to Southern Europe. Various species of Lathyrus (incl. Orobus) occur wild in woods: *L. odoratus* and others are cultivated.

Tribe 9. *Phaseoleæ.* Stamens diadelphous: legume unilocular; cotyledons usually epigean, but not leafy: leaves usually imparipinnate, frequently ternate. Mostly climbing plants with twining stems.

Phaseolus vulgaris, the French Bean, and *P. multiflorus*, the Scarlet Runner, are cultivated. *Wistaria* (*Glycine*) *chinensis* is an ornamental climber. Physostigma is the Calabar Bean.

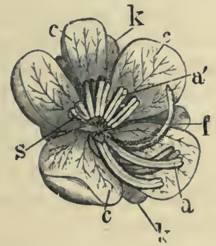

FIG. 436.—Flower of a Cassia: *k* calyx; *c* corolla; *a* stamens; *a'* the central shorter ones; *f* ovary.

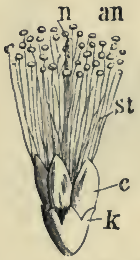

FIG. 437.—Flower of an Acacia (mag.): *k* calyx; *c* corolla; *st* stamens, with (*an*) anthers; *n* stigma.

Tribe 10. *Dalbergieæ.* Stamens mono- or dia-delphous: legume indehiscent; cotyledons fleshy.

Pterocarpus. *Dipteryx odorata*, the Tonka Bean of South America, contains coumarin in the seed.

Sub-order 2. CÆSALPINIEÆ. Flower dorsiventral, but not papilionaceous (Fig. 327 *B* and Fig. 436); petals imbricate so that the posterior petal is overlapped by those anterior to it; stamens ten or fewer, free, more rarely connate: the legume is frequently divided by transverse septa, and is indehiscent: flowers in panicles or racemes: seeds often albuminous.

Gleditschia triacanthos and other species are culivated for ornament. *Cercis Siliquastrum*, the Judas tree, has rounded leaves. The wood of *Cæsalpinia braziliensis* is known as Pernambuco or Brazil wood. Hæmatoxylon, Cassia, Bauhinia, Tamarindus, and Ceratonia (*C. Siliqua*, the Carob-tree) are other well-known genera.

Sub-order 3. MIMOSEÆ. Flowers regular; petals with valvate æstivation (see Fig. 321): stamens ten, rarely fewer, frequently very numerous, free (Fig. 437), usually much longer than the perianth: legume sometimes divided by transverse septa: seed rarely albuminous: flowers usually grouped in spikes or capitula.

Mimosa pudica, the Sensitive Plant, has irritable leaves. Species of Acacia are numerous in Africa, Asia, and Australia. In the Australian species the leaves are represented by flattened petioles (phyllodes, p. 49) which are extended in the median plane.

Order 3. PLATANACEÆ. Trees, with diclinous flowers in capitula borne laterally on pendulous branches; flower perigynous, perianth differentiated into calyx and corolla, 3–4-merous: andrœcium of but few stamens: gynæceum apocarpous; each ovary contains usually a single ovule, and developes into a caryopsis; seed suspended, orthotropous, with but little endosperm: leaves scattered, with persistent sheathing stipules.

FIG. 438. ♀ flower of Platanus (mag.).

Platanus occidentalis, from North America, with three-lobed leaves, and *P. orientalis*, from the East, with usually five-lobed leaves, which are often cuneiform at the base, are frequently cultivated (especially the former). The smooth bark, which is shed in flakes, is very characteristic (p. 212). The Plane may be at once distinguished from the Maples, which resemble it a good deal in the form of the leaf, by the scattered arrangement of the leaves.

Cohort V. **Saxifragales.** Flowers generally ambisporangiate and actinomorphic; hypogynous, perigynous or epigynous; eucyclic; stamens usually in two whorls, with obdiplostemony; ovary generally syncarpous, multilocular, with more than one style or stigma; ovules usually numerous in each loculus; seed with or without endosperm.

Order 1. SAXIFRAGACEÆ. Flowers usually 4–5-merous, epigynous or perigynous, completely actinomorphic only when there are five carpels: stamens usually in two whorls; carpels less numerous, usually connate below and free above; seeds numerous, containing endosperm.

Tribe 1. *Saxifrageæ.* Flowers perigynous or epigynous, regular, but generally zygomorphic in consequence of oligomery in the gynæceum: petals with imbricate æstivation, sometimes suppressed: two whorls of stamens, but one or other of the whorls is suppressed in some genera and species: carpels usually two, diverging above (Fig. 335 *D*): inflorescence of racemose cymes: fruit a capsule: leaves alternate.

The British genera are Saxifraga and Chrysosplenium:—Saxifraga has an oblique bilocular ovary, and the flower is consequently obliquely zygomorphic (Fig. 324 *C*); the receptacle invests the lower connate portion of the ovary: many species occur in mountainous districts, and in several of them there is a deposit of carbonate of lime on the margins of the leaves (see Fig. 100, p. 139); only a few species, such as *S. tridactylites* and *granulata*, occur in the plains: Chrysosplenium, the Golden Saxifrage, has a tetramerous flower destitute of a corolla; they are small plants, somewhat resembling a Euphorbia, occurring in damp places. Among the more familiar cultivated genera are Astilbe (Hoteia), Rodgersia, Bergenia (Fig. 439), Tiarella, Heuchera, etc.

Tribe 2. *Parnassieæ.* Flowers perigynous, often actinomorphic; the five stamens opposite to the petals are transformed into glandular staminodes; petals with imbricate æstivation: ovary 4–5-merous, unilocular: fruit a loculicidal capsule: leaves alternate.

FIG. 439.—Longitudinal section of the ovary of Bergenia: *g* style; *n* stigmata; *p* placentæ (mag.). (After Sachs.)

FIG. 440.—Floral diagram of Parnassia; but the whorl of antipetalous staminodes should be represented as external to the whorl of stamens.

Parnassia palustris, Grass of Parnassus, has a whorl of radical leaves, and terminal and lateral peduncles each bearing a single flower and adnate to a bracteole: it is frequently found in damp localities.

Tribe 3. *Hydrangeæ.* Flowers epigynous, actinomorphic, obdiplostemonous: petals with valvate æstivation: carpels 3–5: shrubs with opposite leaves.

Hydrangea hortensis is a well-known garden plant. The inflorescence is an umbellate panicle, the marginal flowers of which (in cultivated plants all of them) are sterile, having a very much enlarged calyx, and either no stamens or only the whorl of stamens opposite to the sepals.

Tribe 4. *Philadelpheæ.* Flowers epigynous, actinomorphic, 4–5-merous: stamens in two whorls but not obdiplostemonous, or indefinite: petals with various æstivation: fruit a capsule: shrubs with opposite leaves.

Philadelphus coronarius (called Syringa or Mock Orange) has sweetly-scented tetramerous flowers. *Deutzia scabra*, *crenata*, and others are cultivated.

Tribe 5. *Ribesieæ.* Flowers epigynous, incompletely actinomorphic, pentamerous: stamens five, opposite to the sepals; carpels usually two, usually median, sometimes lateral (Fig. 324*B*): fruit a berry: leaves scattered: inflorescence racemose. Shrubs.

Several species of Ribes, the Currant, are cultivated: *R. rubrum* is the Red Currant; *R. nigrum*, the Black Currant; *R. Grossularia*, the Gooseberry: the spines of the last species are developed from the pulvinus.

Various species of Escallonia are cultivated as ornamental flowering shrubs.

Order 2. Crassulaceæ. Formula $K\mathrm{n}, C\mathrm{n}, \mid A\mathrm{n}+\mathrm{n}, G\mathrm{n}$, where $\mathrm{n}=3$—30: flowers actinomorphic, perigynous or hypogynous, with two (rarely one) whorls of stamens: gynæceum, generally completely apocarpous; carpels opposite to the petals, with a scale (disc), external to each carpel: ovules numerous, marginal: fruit a follicle: seed with endosperm: inflorescence usually cymose. Plants with entire fleshy leaves, arranged spirally, often in rosettes.

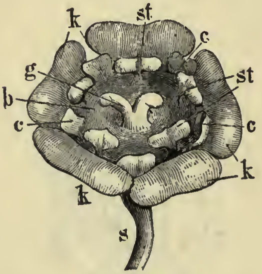

Fig. 441.—Flower of Ribes (mag.): *s* pedicel; *k* calyx; *c* corolla; *st* stamens; *b* disc; *g* styles.

Fig. 442.—Flower of *Sedum acre* (× 3).

The genus Sedum has usually pentamerous flowers; *Sedum acre*, the Stonecrop, is common on walls and rocks; *S. Rhodiola* has diœcious flowers (see Fig. 318). *S. Telephium*, the Orpine and others are common. The genus Sempervivum has at least 6-merous flowers; *S. Tectorum*, the Houseleek, and other species, as also species of Echeveria, Crassula, etc., are frequently cultivated. Tillæa has usually tetramerous flowers without the hypocarpellary scales.

Order 3. Cephalotaceæ. Flowers apetalous, perigynous, 6-merous: stamens in two whorls: gynæceum of six apocarpous carpels, each containing a single basal ovule.

This order consists of the Australian genus Cephalotus, with the single species *C. follicularis*: the lower of the tuft of radical leaves are pitchered and have lids.

Order 4. Pittosporaceæ. Flowers hypogynous: stamens five, antisepalous: carpels 2–5, ovary syncarpous, uni- or multi-locular, with parietal or axile placentation: ovules numerous: seed with endosperm. Shrubs with simple exstipulate leaves, and schizogenous resin-ducts.

Pittosporum Tobira, undulatum, crassifolium, are ornamental shrubs from Australia.

Order 5. HAMAMELIDACEÆ. Flowers frequently diclinous and apetalous, 4–5-merous, perigynous, or nearly epigynous: stamens typically in two whorls, but one or other of the whorls is frequently suppressed: ovary usually bilocular: leaves stipulate.

Hamamelis virginica, the Witch-Hazel, is an ornamental shrub from North America, the leaves of which somewhat resemble those of the Hazel. Other well-known shrubs are Parrotia, Liquidambar, etc.

Order 6. PODOSTEMACEÆ. Small aquatic plants: flowers sometimes diclinous or diœcious: perianth generally much reduced, and sometimes completely suppressed: stamens one or many, sometimes monadelphous: ovary superior, 1- 2- or 3-locular: seeds many.

A very remarkable group of plants, growing on stones, etc., in swiftly flowing streams and rivers of the tropics: so complete is their adaptation to their environment that they have more or less completely assumed the general habit and appearance of Lichens, Algæ, Mosses, and Liverworts.

SUB-CLASS II. GAMOPETALÆ.

Flowers usually ambisporangiate: perianth differentiated into calyx and corolla; calyx usually gamosepalous; corolla generally gamopetalous, in some cases suppressed: ovary usually syncarpous.

SERIES I. HYPOGYNÆ.

Ovary superior (except in Vacciniaceæ): stamens epipetalous, or free and hypogynous.

Cohort I. **Lamiales.** Flower pentamerous, usually dorsiventral: the formula is generally $\downarrow K\ (5)\ (C\ (5)\ A\ 5)\ G^{\underline{(2)}}$; corolla usually bilabiate, the two posterior petals being connate and forming a frequently helmet-shaped (*galeate*) projecting upper lip; the anterior petal, with the two lateral petals, forming the under lip: stamens epipetalous; the posterior stamen is usually suppressed or is a staminode; the two lateral stamens are generally shorter than the two anterior ones, so that the flower is didynamous: the two median carpels form a usually bilocular ovary which sometimes becomes sub-divided into four loculi: leaves scattered, or opposite decussate, exstipulate: the leafy shoots have no terminal flower.

Order 1. LABIATÆ. Stamens four, didynamous (Fig. 443 *B*); rarely, as in Salvia and its allies, only the two anterior stamens are developed: the bicarpellary ovary becomes subdivided by spurious dissepiments into four loculi (see Fig. 450 *C*), which part, as the seed ripens, into four nutlets (Fig. 443 *C*); style gynobasic: the ovule in each loculus is solitary and erect: seed without endosperm. Herbs with decussate leaves and quadrangular stem. The flowers are disposed apparently in whorls round the stem, but the inflorescence is in fact made up of compound cymes or dichasia, termed verticillasters, developed in the axil of each of the two opposite leaves.

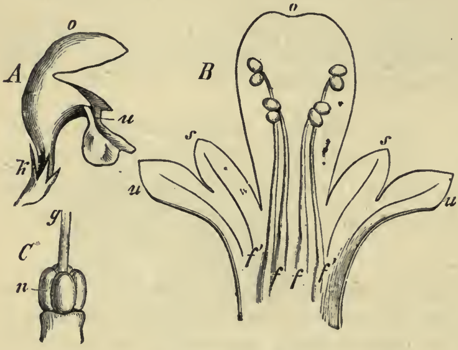

FIG. 443. *A* Flower of Lamium, side view: *k* calyx; *o* upper; *u* under lip. *B* Flower of Leonurus opened: *o* upper: *u* divided under lip; *s* lateral lobes of the corolla; *f f* short, *f' f'* long stamens (mag.). *C* Gynæceum; *n* 4-lobed ovary; *g* style (mag.).

Tribe 1. *Ocimoideæ.* Stamens 4, descending.

Ocimum basilicum, the Sweet Basil, from India, and Lavandula, the Lavender from Southern Europe, are cultivated as pot-herbs: several species of Coleus are cultivated.

Tribe 2. *Menthoideæ.* Stamens 4, equal, ascending, divergent: corolla almost regular, 4- or 5-lobed.

Many species of Mentha, Mint, are common. *Pogostemon Patchouli* yields oil of Patchouli. Lycopus has only 2 fertile stamens, the two posterior ones being abortive.

Tribe 3. *Satureineæ.* Stamens 4, with broad connective, ascending, either almost equal (Thymus, Origanum), or didynamous and remote at base, conniving under the upper lip.

Origanum vulgare is the Wild Marjoram; the Sweet Marjoram which is cultivated is an exotic species. *Thymus Serpyllum* is the wild Thyme; the garden Thyme is *T. vulgaris*, from Southern Europe. *Satureia hortensis* (exotic) is the Summer Savory. Various species of Calamintha (stamens not divergent) are common, such as *C. arvensis*, the Common Basil, and *C. Clinopodium*, the Wild Basil.

Tribe 4. *Melissineæ.* Stamens 4, didynamous, with narrow connective, remote at base, conniving under upper lip.

Melissa officinalis, the Balm, and Hyssopus, the Hyssop, are cultivated as pot-herbs.

Tribe 5. *Monardeæ.* Stamens 2, ascending: one theca of each anther is either wanting or it is widely separated from the other (see Fig. 331*C*).

Salvia verbenacea, the Wild Sage or Clary, is common. *Rosmarinus officinalis*, the common Rosemary, is exotic.

Tribe 6. *Nepeteæ.* Stamens 4, didynamous, ascending, parallel; the posterior two are the longer.

Nepeta Cataria, the Catmint, occurs in hedges; and *Nepeta Glechoma*, the Ground Ivy, is very common.

Tribe 7. *Stachydeæ.* Stamens 4, didynamous, ascending, parallel; the anterior two are the longer: upper lip of corolla usually arched (ringent).

Lamium album, the Dead-Nettle, and *purpureum*, are very common. Various species of Galeopsis (Hemp-Nettle), Stachys (Woundwort or Betony), Marrubium (Horehound), Ballota, Melittis, and Leonurus (Mother-wort) are found in England.

Tribe 8. *Scutellarieæ.* Stamens 4, didynamous, ascending, parallel; calyx closed when the fruit is ripe.

In the genus Scutellaria, the anthers of the anterior pair of stamens have but one theca; *S. galericulata*, the common Skullcap, and *S. minor*, the Lesser Skullcap, are common. In the genus Prunella each filament has a small tooth below the anther: *P. vulgaris* is common.

Tribe 9. *Ajugoideæ.* Stamens 4, didynamous, ascending, parallel; the posterior two are the shorter: upper lip of corolla very short.

Ajuga reptans, the Creeping Bugle, and *Teucrium Scorodonia*, the Wood Germander, are common.

Order 2. VERBENACEÆ. Flower sometimes regular: stamens four, didynamous, or two: ovary 1- or 2-locular, with two ovules in each loculus, or spuriously 2- or 4-locular in consequence of the presence of false dissepiments, with one ovule in each loculus: endosperm small or absent: the fruit separates into 2–4 nutlets: style terminal: leaves usually opposite.

Verbena officinalis, the Vervain, is common on waste ground and roadsides: *V. Aubletia* is a common garden plant. *Tectona grandis*, the Teak-tree of the East Indies, has a hard wood used in ship-building. *Vitex Agnus castus*, the Chaste or Hemp-tree, is an ornamental cultivated shrub.

Order 3. GLOBULARIACEÆ. Stamens four, didynamous: ovary unilocular, with one suspended ovule: style lateral: seed with endosperm: leaves scattered: inflorescence capitulate.

Globularia vulgaris and *cordifolia*, with radical leaves, occur here and there in dry places on the Continent.

Cohort II. **Personales.** Flowers pentamerous, usually dorsiventral: stamens epipetalous: the posterior stamen is usually suppressed, or appears as a staminode: carpels 2, median: ovules usually indefinite.

Order 1. SCROPHULARIACEÆ. Ovary bilocular, with numerous anatropous ovules borne on axile placentæ: seed with endosperm: stamens four, didydamous, often with a rudimentary fifth posterior stamen (Fig. 445 *B*, *st*); sometimes only the two lateral stamens are present; rarely all five are fertile: corolla with imbricate (cochlear) æstivation: general floral formula as in Lamiales.

Sub-order 1. PSEUDOSOLANEÆ. Flower nearly regular: the two posterior petals are external, the anterior internal: stamens usually 5: leaves scattered. The genus Celsia has only 4 stamens. In the British species of the genus Verbascum, *V. Thapsus*, the great Mullein, has unequal stamens, the two anterior being longer and glabrous, whilst the three posterior are short and their filaments have white hairs; the stamens are similarly unequal in *V. virgatum* and in *V. Blattaria*, but here the hairs are purple and are present (though fewer) on the filaments of the long stamens: in *V. Lychnitis*, *nigrum*, and *pulverulentum* the stamens are all similar, the hairs being purple in *V. nigrum* and white in the two other species.

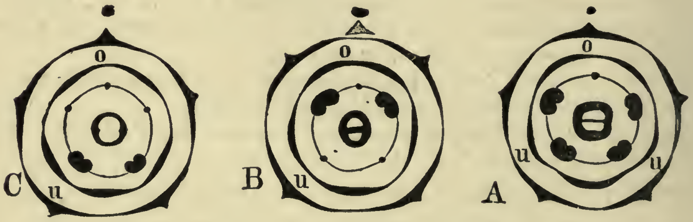

FIG. 444.—Floral diagrams, *A* of most Scrophulariaceæ; *B* of Veronica; *C* of the Lentibulariaceæ: *o* upper, *u* under lip.

Sub-order 2. ANTIRRHOIDEÆ. Flowers irregular: corolla as in the preceding, the two posterior petals forming the upper lip of the corolla: stamens 4: leaves opposite. Antirrhinum, the Snapdragon, has a projection on the lower lip of the personate corolla, termed the palate; the corolla is gibbous at the base; stamens 4 (Fig. 445 *A B*): *A. majus*, the great Snapdragon, is a well-known garden plant. Linaria has a spurred personate corolla; stamens 4: *L. vulgaris*, the yellow Toad-Flax, is common in fields. In Gratiola the two anterior stamens are represented by staminodes. *Paulownia imperialis* is an ornamental flowering tree from Japan. Limosella (*L. aquatica*, the Mudwort) has a subcampanulate corolla with a short tube. Mimulus (*M. luteus*, the Yellow Monkey-flower) has a subcampanulate corolla with a two-lipped limb; the two lobes of the stigma close together on being touched. Maurandia and Rhodochiton are genera of plants climbing by means of sensitive petioles. Many species of Mimulus (Musk), Calceolaria, Chelone, and Pentstemon, are cultivated.

Sub-order 3. RHINANTHOIDEÆ. Flower irregular: the two posterior petals are overlapped by the lateral petals: stamens 4, or 2. Digitalis, the Foxglove, has an obliquely campanulate (digitaliform) corolla; stamens 4: *D. purpurea* is common in woods; the yellow *D. grandiflora* is cultivated. Scrophularia has a globose corolla; *S. nodosa* (Figwort) and *S. aquatica* are common. Veronica, the Speedwell, has only the 2 postero-lateral stamens, and the two lobes of the upper lip of the (rotate) corolla are united; the posterior lobe of the calyx is suppressed (Figs. 444 *B*, 445 *C*): *V. Anagallis* and *V. Beccabunga* are common in ditches; *V. arvensis*, *agrestis*, *serpyllifolia*, *Chamædrys*, and others in pastures and fields. Sibthorpia has a sub-rotate 5–8-fid corolla, and four stamens; *S. europæa* is the Cornish Moneywort.

Pedicularis, the Lousewort, has a 5-toothed calyx, and the upper lip of the corolla is galeate: Euphrasia, the Eyebright, has a 4-toothed calyx, the upper lip of the corolla has two spreading or reflexed lobes: Bartsia has a 4-toothed calyx, upper lip of the ringent corolla entire or only notched: Rhinanthus, the Rattle, has a four-toothed inflated calyx: Melampyrum, the Cow-Wheat, has a 4-toothed tubular calyx, and the capsule is few-seeded: all these plants possess chlorophyll, but they are more or less parasitic upon the roots of other plants.

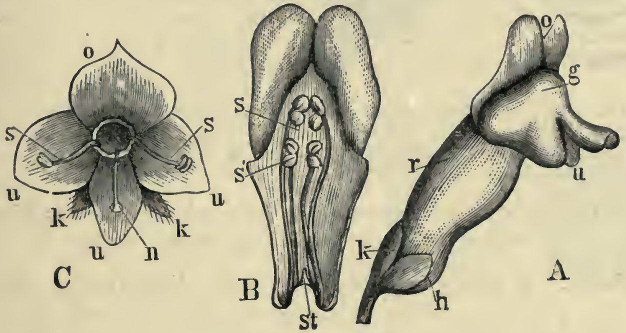

FIG. 445.—Flowers of Scrophulariaceæ. *A* Antirrhinum: *k* calyx; *r* tube of the personate corolla, gibbous at the base (*h*); *o* upper, *u* under lip of the corolla; *g* prominence palate) of the under lip. *B* Upper lip of the same, seen from within: *s* the two longer anterior stamens; *s′* the short lateral ones; *st* rudimentary posterior one. *C* Flower of Veronica: *k* calyx; *u u u* the three lobes of the lower lip of the rotate corolla: *o* the upper lip; *s s* the two stamens; *n* stigma.

Order 2. PLANTAGINACEÆ. Flowers regular, isobilateral, and apparently tetramerous, but the true interpretation of them is deduced from those of Veronica (Figs. 444 *B* and 446): the posterior sepal is suppressed, as also the posterior stamen; the two posterior petals cohere to form an upper lip which is quite similar to one of the lobes of the three-lobed lower lip (Fig. 445 *C*): stamens four, the two anterior not being suppressed: ovary dimerous, bilocular, or sometimes unilocular or spuriously 4–locular: ovules solitary and basal, or numerous: fruit a capsule with transverse dehiscence, or a nutlet: seed with endosperm.

Plantago lanceolata (Ribwort), *major*, *media*, the Plantains, are weeds universally distributed. *P. Coronopus*, the Buck's-horn Plantain, and *P. maritima*, grow in dry places and on sandy sea-shores. The leaves form a rosette just above the root, and the long scapes spring from their axils, bearing simple spikes (Fig. 446 *a*, *d*). In *P. Cynops*, *Psyllium*, and others, the main stem is elongated: the testa of the seed is mucilaginous. In *Littorella lacustris* the flowers are monœcious; fruit 1-seeded, indehiscent; stamens hypogynous: it grows on the bottom in shallow waters.

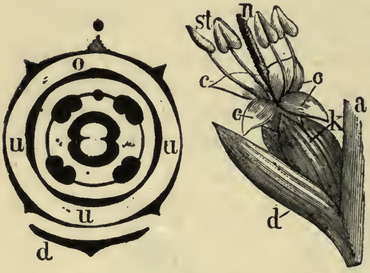

FIG. 446.—Flower of Plantago: *a* axis of the inflorescence (scape); *d* bract; *k* calyx; *c* corolla; *st* stamens; *n* stigma (mag.). In the diagram, *o* is the upper, and *u* the under lip.

Order 3. BIGNONIACEÆ. Stamens generally four, didynamous: ovary bilocular or unilocular: seeds usually winged, without endosperm. Woody plants; frequently climbers, by means of twining stems, or leaf-tendrils, or roots (Tecoma).

Catalpa bignonioides is an ornamental tree from North America: Bignonia, Tecoma, and Eccremocarpus, are well-known cultivated climbers.

Order 4. ACANTHACEÆ. Stamens four, didynamous (diagram as in Fig. 444 *A*): ovary bilocular: ovules few on projecting placentæ: seed without endosperm. Herbs.

Acanthus mollis and other species from Southern Europe, are ornamental plants: Thunbergia and Ruellia are commonly cultivated: Adhatoda, Justicia, and others have only the two antero-lateral stamens (as in Fig. 444 *C*).

Order 5. GESNERACEÆ. Stamens usually four, didynamous, or sometimes two only: ovary unilocular, with numerous parietal ovules: seed with or without endosperm. Generally herbs with opposite leaves.

Columnea, Gloxinia, Achimenes, Sinningia, Streptocarpus, and others, are ornamental plants from tropical America: Ramondia inhabits the mountains of Southern Europe.

Order 6. OROBANCHACEÆ. Plants which are destitute of chlorophyll, with scaly leaves, parasitic on the roots of other plants: otherwise similar to the Gesneraceæ.

The commoner species of Broomrapes, occurring in Britain, are *Orobanche major* and *minor*, parasitic on Leguminosæ, *elatior* on the Greater Knapweed, *Hederæ* on Ivy, *ramosa* on Hemp; mostly of a brownish or whitish hue. *Lathræa Squamaria*, the Greater Toothwort, is generally parasitic on the roots of the Hazel: it is of a pale rose colour with slightly bluish flowers: the subterranean scaly leaves each form a kind of pitcher apparently for the purpose of catching insects.

Order 7. LENTIBULARIACEÆ. Only the two antero-lateral stamens are developed (Fig. 444 *C*): ovary unilocular: ovules numerous on a free central placenta: seed without endosperm.

The numerous species of Utricularia are floating water-plants with finely divided leaves bearing bladder-like appendages (modified leaflets) which serve to catch small aquatic animals (Fig. 447). *Pinguicula vulgaris* and *alpina* (Butterworts) are small plants growing in damp places, with rosettes of radical leaves which catch insects by their viscid secretion.

Cohort III. **Polemoniales.** Flowers generally regular, but zygomorphic in consequence of oligomery in the gynæceum; pentamerous: stamens epipetalous: ovary of two, rarely five, carpels: leaves usually scattered and exstipulate: the inflorescence is often cymose, with a terminal flower: formula $K(5)\ (C(5)\ A5)\ G^{\underline{(2)}}$ to $(^{\underline{5}})$.

Order 1. CONVOLVULACEÆ. Usually two median carpels forming a bilocular ovary, with 1–2 anatropous ovules in each loculus: the corolla has usually a contorted æstivation, twisted to the right: fruit a septifragal capsule, or a berry: seed with endosperm. Commonly plants climbing by twining stems: with milky latex.

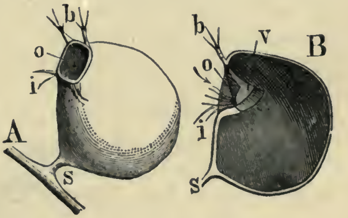

FIG. 447.—Bladders of Utricularia. *A* Outside view: *s* pedicel; *o* entrance; *i* and *b* bristly appendages. *B* Section: *v* a valve opening inwards and preventing the exit of the imprisoned animal (mag.).

Convolvulus arvensis, the lesser Bindweed (Fig. 329 *A*), and *Calystegia Sepium*, the larger Bindweed, the former with two small bracteoles, the latter with two large bracteoles which invest the calyx, and *C. Soldanella*, the Sea-Bindweed, are common wild plants. *Batatas edulis* is cultivated in tropical America for its edible tuberous rhizome, the Sweet Potato.

The genus Cuscuta consists of parasites destitute of chlorophyll, with filiform twining stems, which attach themselves to other plants by means of haustoria (see p. 66), and derive their nourishment from them: the small flowers are arranged in fascicles (Fig. 448 *b*): the corolla has imbricate æstivation: fruit a capsule with transverse dehiscence.

Cuscuta europæa, the greater Dodder, which occurs commonly on Nettles and Hops, is widely distributed: *C. Epilinum* is the Flax Dodder, and *C. Epithymum*, the lesser Dodder, occurs on various low-growing plants; *C. Trifolii* attacks Clover, which it often destroys.

Order 2. Polemoniaceæ. Ovary usually trimerous and trilocular, with one erect or several oblique ovules in each loculus: capsule loculicidal: seed with endosperm. Mostly herbs.

Polemonium cæruleum is Jacob's Ladder; various species of Phlox and Gilia are common garden plants. Cobæa is a genus of plants climbing by means of leaf-tendrils.

Order 3. Solanaceæ. Ovary usually consists of two obliquely placed carpels (Fig. 324 *D*), bilocular, with numerous ovules in each loculus; the axile placentæ sometimes project so far into the loculi that the ovary appears to be quadrilocular, as in Datura: ovules campylotropous; fruit a capsule with various dehiscence, or a berry: seed with endosperm. Herbs, occasionally woody plants, sometimes climbers by irritable petioles (*e.g.* species of Solanum); without milky latex. Inflorescence cymose, but complicated by the displacement of the bracts: Fig. 449 *B*, for instance, is a diagram of the inflorescence of Atropa; the main axis which terminates with the flower 1, bears a bracteole 1α and a lateral shoot terminating in the flower 2; this springs from the axil of a bract

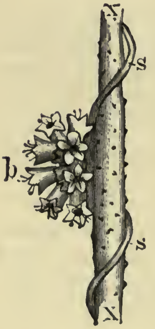

Fig. 448. — Stem of *Cuscuta europæa* (*s*), with inflorescence (*b*) twining round a stem of Hop (*x*).

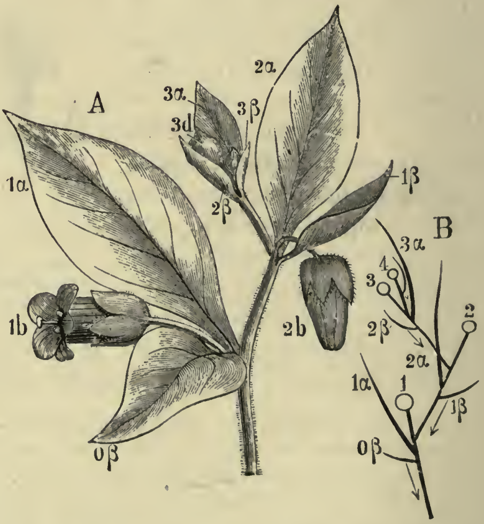

Fig. 449.—*A* Upper portion of a flowering stem of *Atropa Belladonna*. *B* Diagram of the same stem: 1 2 3 the flowers; α and β the bracteoles and bracts. From the axils of β spring the new floral axes, along which the bract β is displaced.

1β, which, however, is not inserted at the base of its axillary shoot (the point of the arrow indicates its proper position), but is displaced upwards until it is close under the bracteole 2α; this displacement is repeated throughout the whole system of the cyme, so that in Atropa there are always two leaves below each flower, a larger one (Fig. 449 *A* 1α, 2α, and so on) which is the bracteole of the flower, and a smaller one (Fig. 449 *A* 0β, 1β, 2β, etc.,) which is the bract from the axil of which the flowering-shoot springs. In other of the Solaneæ similar arrangements are found. Most plants of this order are poisonous.

Tribe 1. *Solaneæ.* Fruit a berry : embryo curved. In the genus Solanum the anthers are syngenesious : *S. Dulcamara*, the Bittersweet or Woody Nightshade, has a blue flower, and *S. nigrum* has a white flower ; both are common : *S. tuberosum* is the Potato-plant. *Physalis Alkekengi*, the Winter Cherry, has an inflated red calyx which encloses the berry. *Lycopersicum esculentum* is the Tomato. The fruits of *Capsicum longum* and *annuum* are known as Chili Peppers. *Atropa Belladonna* is the Deadly Nightshade ; the anthers are not syngenesious, and the corolla is campanulate ; the berries are black and very poisonous. *Lycium barbarum* is a shrub belonging to Southern Europe which has become wild in places in the North. *Hyoscyamus niger* is the common Henbane : the capsule dehisces transversely (pyxidium).

Tribe 2. *Datureæ.* Capsule almost quadrilocular in consequence of the outgrowth of the placenta, 4-valved : embryo curved. *Datura Stramonium* is the Thorn-apple.

Tribe 3. *Cestreæ.* Embryo straight : all five stamens fertile. *Nicotiana Tabacum* is the Tobacco plant (Fig. 329 *B*) : Petunia is commonly cultivated (Fig. 324 *D*) : Cestrum is a well-known genus of greenhouse shrubs.

Tribe 4. *Salpiglossideæ.* Embryo straight : stamens unequal, only 2 or 4 fertile. The tribe includes many cultivated herbaceous or shrubby plants, such as Salpiglossis, Schizanthus, Browallia, Streptosolen.

Order 4. BORAGINACEÆ. Ovary consisting of two median carpels, spuriously quadrilocular in consequence of a constriction along the dorsal suture of each carpel (Fig. 450 *C*, *r*) : the single style usually arises from the incurved apices of the carpels (gynobasic), and is surrounded at its base by the four loculi (Fig. 450 *B*) : each loculus contains a single suspended anatropous ovule : when the fruit is ripe the loculi separate completely, and appear to be four nutlets : seed without endosperm : the corolla usually has five scaly ligular appendages at the junction of the limb with the tube (Fig. 450 *A* *b*) : inflorescence scorpioid (see p. 492), often very complicated. Herbs or shrubs generally covered with harsh hairs and only rarely glabrous, *e.g. Myosotis palustris*.

Sub-order 1. Ehretoideæ. Style at the apex of the ovary.

Heliotropium peruvianum, is a well-known garden plant with fragrant flowers.

Sub-order 2. Boraginoideæ. Style inserted between the four lobes of the ovary (gynobasic).

Myosotis is the Scorpion-grass; *M. palustris*, the Forget-me-not, occurs in damp places, *M. sylvatica* in woods, and *M. arvensis* and others in fields. *Lithospermum arvense* (Gromwell), *L. officinale*, *Echium vulgare* (Viper's Bugloss), with an irregular flower, *Symphytum officinale*, the Comfrey, *Lycopsis arvensis* (Common Bugloss), *Cynoglossum officinale* (Hound's-tongue), and *Borago officinalis*, the Borage, are common. *Anchusa officinalis*, the Alkanet; *Mertensia maritima*, the smooth Gromwell or Sea-Bugloss; and *Pulmonaria angustifolia*, the Lung-wort, are rare in Britain.

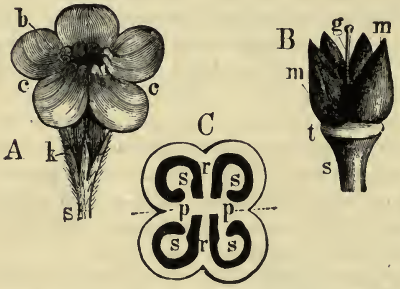

Fig. 450.—*A* Flower of Anchusa (slightly mag.): *k* calyx; *c* corolla; *b* the scaly appendages. *B* Fruit of Myosotis (mag.); *t* the receptacle; *m m* the four achænia; *g* the gynobasic style. *C* Diagram of the quadrilocular ovary in trans. section: *r* the dorsal sutures; *p p* the placentæ; *s* the ovules.

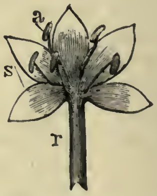

Fig. 451. — Corolla of *Erythræa Centaurium* spread out: *r* tube; *s* limb; *a* stamens.

Cohort IV. **Gentianales.** Flowers regular, zygomorphic in consequence of oligomery in the gynæceum (see Fig. 324): perianth and andrœcium usually 4- or 5-merous: corolla with frequently contorted æstivation (to the right): stamens inserted on the tube of the corolla: carpels two: leaves commonly decussate and exstipulate: formula $K\,(5)\ (C\,(5)\ A\,5)\ G^{\underline{(2)}}$.

Order 1. Gentianaceæ. Carpels perfectly connate, forming a uni- or incompletely bi-locular ovary: ovules parietal, numerous, anatropous: seed with endosperm. Usually herbs without milky latex: leaves almost always entire.

Sub-order 1. Gentianeæ. Leaves decussate: corolla with contorted æstivation.

Gentiana (Fig. 324 *E*), the Gentian, has a bilobed stigma; it occurs in mountainous districts. Erythræa has a capitate stigma; *E. Centaurium*, the common Centaury, is common in pastures (Fig. 451). Species of Cicendia and Chlora also occur in Britain.

Sub-order 2. **Menyantheæ.** Leaves spiral: corolla with valvate æstivation.

Menyanthes trifoliata, the Buck-bean or Bog-bean, with ternate leaves, is common in marshes (Fig. 324 *F*): *Villarsia nymphæoides* (or *Limnanthemum peltatum*) is found in ponds and rivers.

Order 2. Loganiaceæ. Corolla with usually valvate æstivation: ovary usually bilocular, each loculus containing one or several ovules: seed with endosperm (Fig. 295 *A*). Mostly trees with opposite and usually exstipulate leaves; some are climbers with either twining stems (*e.g.* Fagræa, Gelsemium), or stem-tendrils (species of Strychnos).

Semen Strychni, or *Nux vomica*, the seed of *Strychnos Nux vomica*, in the East Indies, is extremely poisonous. The South American Indians poison their arrows with a substance known as Curare, in the preparation of which the cortex of species of Strychnos is used.

Order 3. Apocynaceæ. Corolla with contorted æstivation. The two carpels are usually connate only by their styles, which become free as they ripen: seed usually devoid of endosperm. Herbs or shrubs, sometimes climbers, with milky latex.

Vinca minor (see Fig. 324 *A*) and other species, the Periwinkles, are common creeping plants, wild and in gardens. *Nerium Oleander*, an ornamental shrub, and species of other genera (*e.g.* Allamanda, Landolphia, Amsonia, Dipladenia) are often cultivated: Allamanda and Dipladenia include scrambling species, climbing by means of hooks: Allamanda has a unilocular ovary with two parietal placentæ.

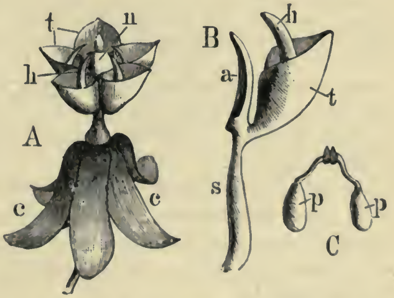

Fig. 452.—*A* Flower of Asclepias (mag.): *c* the reflexed corolla; *n* stigma; *h* the spurs, *t* the pouches, of the stamens. *B* A solitary stamen; *a* the anther. *C* Pollen-masses, *p* and *p*.

Order 4. Asclepiadaceæ. Corolla with usually imbricate æstivation. The two carpels usually form two distinct monomerous ovaries: styles short, united into one stigma: stamens connate, forming a tube surrounding the gynæceum, having pouch-shaped (Fig. 452 *A B*, *t*) and spur-shaped (Fig. 452 *A B*, *h*) appendages: anthers 2–4 locular; the pollen of each sac forms a mass (pollinium, see p. 434), and the masses of each pair of contiguous sacs adhere (Fig. 452 *C*, *p*, *p*) and are conveyed by insects to the stigmata: ovules numerous, attached to the ventral suture: seed usually without endosperm. Generally woody plants, often climbers, with milky latex.

Asclepias syriaca and other species are grown in gardens. Stapelia has a fleshy cactus-like stem. *Hoya carnosa*, the Wax flower, *Periploca græca* and *Ceropegia Gardneri*, are cultivated climbing plants with twining stems.

Order 5. Oleaceæ. Calyx and corolla usually 4-merous, sometimes wanting; stamens and carpels two, alternate: ovary bilocular: ovules 2 in each loculus: fruit a capsule, a berry, a drupe, or a samara: seeds 1–4, usually with endosperm: stem woody: leaves always decussate.

Sub-order 1. Oleineæ. Fruit a berry or a drupe: seed suspended.

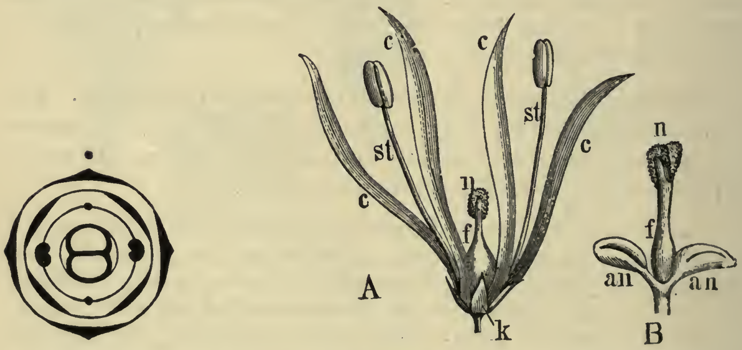

Fig. 453.—*A* Flower of *Fraxinus Ornus* (enlarged): *k* calyx; *c* corolla; *st* stamens; *f* ovary; *n* stigma. *B* ☿-flower of *Fraxinus excelsior*, the common Ash; *an* anthers; *f* ovary; *n* stigma (enlarged). Floral diagram of the Oleaceæ.

Ligustrum has a baccate fruit; *L. vulgare*, the Privet, is a common shrub. Olea has a drupaceous fruit; *O. europæa* is the Olive-tree of the East and of Southern Europe. Phillyrea, Osmanthus, and Chionanthus, are cultivated as ornamental shrubs.

Sub-order 2. Fraxineæ. Fruit a samara: seed suspended.

The genus Fraxinus has a winged fruit; in *F. excelsior*, the common Ash, the perianth is suppressed and the flowers are polygamous; in *F. Ornus*, the Manna-Ash of Southern Europe, the perianth is complete, and the corolla is deeply cleft (Fig. 453 *A*).

Sub-order 3. Syringeæ. Fruit a loculicidal capsule: seed suspended. The genus Syringa has a tubular corolla with a 4-lobed limb; *S. vulgaris* is the Lilac: Forsythia is a well-known shrub, having numerous seeds.

Sub-order 4. Jasmineæ. Fruit a constricted capsule or berry: ovules ascending: seeds exalbuminous: calyx and corolla often 5–10-merous (see Fig. 320).

The flowers of *Jasminum grandiflorum* and other species belonging to Southern Europe, contain a very fragrant ethereal oil.

Cohort V. **Ebenales.** Flowers actinomorphic, 4–8-merous; formula often $K(4)\ C(4)\ A4+4,\ G^{\underline{(4)}}$, the outer (antisepalous) stamens being sometimes suppressed: stamens epipetalous: carpels opposite to the sepals: ovary multilocular, with one or two suspended ovules in each loculus: fruit usually fleshy: seed usually with endosperm.

Order 1. SAPOTACEÆ. Tropical trees with latex in sacs.

The latex of species of Palaquium, Isonandra, Mimusops, etc., constitutes gutta-percha.

Order 2. EBENACEÆ. Trees; flowers generally diclinous.

Diospyros Ebenum in the East Indies, and other species in different parts of the world, yield the wood known as Ebony: *D. Kaki*, the Persimmon, has an edible fruit.

Order 3. STYRACEÆ. Flowers perigynous or epigynous: trees.

Gum Benzoin is the resin of *Styrax Benzoin* in the East Indies: *Halesia tetraptera* the Snowdrop-tree, is a shrub frequently cultivated.

Cohort VI. **Primulales.** Flowers actinomorphic, usually pentamerous: formula $K(5)\ (C(5)\ A0+5)\ G^{\underline{(5)}}$: stamens inserted on the tube of the corolla and opposite to its lobes: gynæceum consisting of five connate carpels which are opposite to the sepals; ovary unilocular, with a free central placenta or a single central ovule: seed with endosperm.

Order 1. PRIMULACEÆ. Style single: ovules indefinite, on a free central placenta (Fig. 338 *G*): the corolla is gamopetalous, tubular below, expanding above into a 5-lobed limb; it is suppressed in the genus Glaux: the stamens (Fig. 454 *a*) are generally adnate to the tube of the corolla and are opposite to its lobes; this position of the stamens is explained by assuming the suppression of an outer antisepalous whorl of stamens which is represented in some genera (*e.g.* Soldanella) and in the following order by petaloid staminodes, an assumption which is confirmed by the analogy of those Ebenales in which the outer whorl of stamens is suppressed: fruit a capsule. Herbaceous plants with conspicuous flowers.

The genus Primula has a 5-valved dehiscent capsule, and a 5-cleft calyx. *Primula vulgaris* is the Primrose; *Primula elatior* and *P. veris* are the Oxlip and the Cowslip or Paigle; they are remarkable in that they are heterostyled (see p. 455). The capsule of *Anagallis arvensis*, the Pimpernel, dehisces transversely (pyxidium). *Cyclamen europæum*, the Sow-bread, has an underground tuber; the lobes of the corolla are reflexed. Lysimachia, the yellow

Loosestrife, has a deeply 5-cleft calyx. Trientalis, the Chickweed Wintergreen, has usually a 7-merous flower. The other British genera are Hottonia (*H. palustris*, the Water-violet), Samolus (*S. Valerandi*, the Brookweed), and Glaux (*G. maritima*, the Sea Milk-wort).

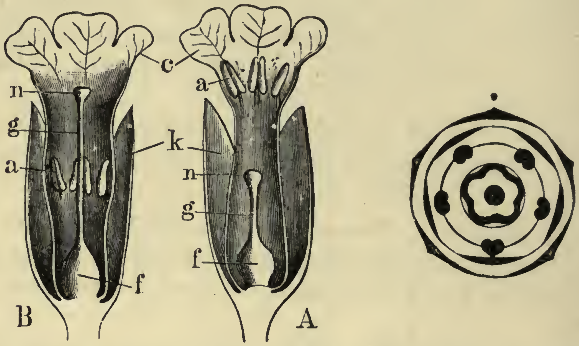

FIG. 454.—Dimorphic flowers of *Primula elatior* in longitudinal section. *A* Short-styled, *B* long-styled form; *k* calyx; *c* corolla; *a* anthers; *f* ovary; *g* style; *n* stigma. Floral diagram of Primula.

Order 2. MYRSINACEÆ. These plants differ from the preceding in that the fruit is baccate and the stem woody: a whorl of staminodes alternating with the petals is present in some genera (*e.g.* Theophrasta).

Ardisia, with red berries, is a well-known ornamental plant.

Order 3. PLUMBAGINACEÆ. Styles five: there is a single basal ovule in the cavity of the ovary, pendulous on a long funicle: flowers often small, in dense inflorescences with numerous bracts: no trace of an external antisepalous whorl of stamens.

In the genus Armeria the flowers are in capitula of scorpioid cymes, which are surrounded by an involucre formed of the lower scarious bracts with downward prolongations embracing the peduncle; *A. maritima*, the Thrift, occurs on sandy soils. *Statice Limonium*, the Sea-Lavender, with racemose cymes, occurs on sandy sea-shores. Plumbago occurs in Southern Europe and in the East Indies.

Cohort VII. **Ericales.** Flowers 4–5-merous, actinomorphic: stamens usually in two whorls and then obdiplostemonous, usually hypogynous: carpels opposite to the petals: formula $K(n)$, $C(n)$, $A\,n+n$, $G(n)$, where $n=4$ or 5: ovary superior or inferior, multilocular, with large recurved axile placentæ: seed with endosperm: anthers sometimes appendiculate (Fig. 332 *B*).

Order 1. ERICACEÆ. Anthers generally opening by two pores at the top (Fig. 455 *A*), often furnished with appendages: pollen in tetrads: fruit a capsule, or succulent: a well-developed disc.

Sub-order 1. RHODODENDROIDEÆ. Fruit a septicidal capsule; corolla fugacious: anthers without appendages.

Rhododendron ferrugineum and *hirsutum*, the Alpine Roses, are wild on the continent: other species of Rhododendron (incl. Azalea), from the mountains of Asia and North America, as also species of Kalmia from North America, are cultivated. *Daboecia polifolia*, the Irish Menziesia or St. Dabeoc's Heath, *Phyllodoce taxifolia*, the Scottish Menziesia, and *Loiseleuria procumbens*, the trailing Azalea, represent the sub-order in the British Flora.

Sub-order 2. ARBUTOIDEÆ. Fruit a berry, or a drupe, or a loculicidal capsule: corolla fugacious: anthers usually appendiculate.

Andromeda Polifolia, the Marsh Andromeda or Wild Rosemary, occurs in peat-bogs, and *Arctostaphylos Uva Ursi* and *alpina*, the red and the black Bearberry, on the mountains of Scotland. *Arbutus Unedo* is the Strawberry tree of Southern Europe, and Gaultheria is the Aromatic Winter-green.

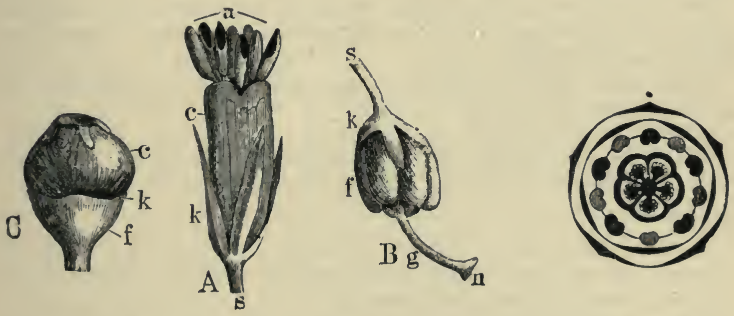

FIG. 455.—*A* Flower of Erica: *s* pedicel; *k* calyx; *c* corolla; *a* anthers. *B* Fruit of *Pyrola rotundifolia*: *s* pedicel; *k* calyx; *f* fruit, the loculi of which alternate with the sepals; *g* style; *n* stigma. *C* Flower of *Vaccinium Myrtillus*: *f* ovary (inferior); *k* calyx; *c* corolla. Floral diagram of Erica: the stamens opposite to the petals are faintly shaded.

Sub-order 3. ERICOIDEÆ. Fruit usually a loculicidal capsule: corolla persistent: anthers usually appendiculate.

Calluna Erica, the Ling or Heather, with a septicidal capsule and a deeply 4-partite coloured calyx, is common on moors: the principal British species of Erica, are *E. mediterranea* (or *carnea*), the Irish Heath; *E. Tetralix*, the cross-leaved Heath; *E. cinerea*, the grey or fine-leaved Heath; and *E. vagans*, the Cornish Heath. Very many species belong to the Mediterranean region, and to the Cape.

Order 2. EPACRIDACEÆ. The whorl of stamens opposite the petals is usually wanting: the anthers open by one fissure only. Australian plants.

Order 3. DIAPENSIACEÆ. Stamens five, inserted in the throat of the corolla: a whorl of antipetalous staminodes sometimes present: anthers opening by oblique longitudinal slits: ovary trilocular. Low-growing evergreen shrubs.

Diapensia lapponica is a creeping shrub of the far North: Shortia and Galax grow on the mountains of North America.

Order 4. PYROLACEÆ. Sepals more or less distinct: petals commonly connate at the base only: anthers without appendages, dehiscing generally transversely or by pores: fruit a loculicidal capsule: seed minute, with an extremely small embryo consisting of only a few cells, and a relatively massive integument. Saprophytes containing chlorophyll.

Pyrola rotundifolia, *secunda*, *minor*, and *uniflora*, the Winter-greens, are found in woods.

The Monotropeæ are saprophytes devoid of chlorophyll, with scale-like leaves. *Monotropa Hypopitys* (*Hypopitys multiflora*), the Bird's nest, is not very common in England.

Closely allied with the Pyrolaceæ is the order LENNOACEÆ, consisting of a few root-parasites destitute of chlorophyll.

Order 5. VACCINIACEÆ. Ovary inferior (Fig. 455 *C*): anthers with appendages (Fig. 332 *B*), usually opening by two pores: fruit a berry.

Vaccinium Vitis-Idæa is the red Whortleberry or Cowberry; it usually blossoms and bears fruit twice in the year: *V. Myrtillus* is the Bilberry, Blaeberry, or Whortleberry, with deciduous leaves: *V. Oxycoccos* (*Oxycoccos palustris*, or *Schollera Oxycoccos*) is the Cranberry: and *V. uliginosum*, the great Bilberry or Bog-Whortleberry. They are all low shrubs occurring on moors.

SERIES II. EPIGYNÆ.

Ovary inferior.

Cohort I. **Campanales.** Flowers actinomorphic or zygomorphic, pentamerous; formula $K(5)$ $C(5)$ $A(5)$ $G_{\overline{(2)}}$ to $_{\overline{(5)}}$: sepals leafy and narrow: stamens usually free from the corolla, but often connate: ovary multilocular, of two to five carpels, inferior.

Order 1. CAMPANULACEÆ. Flowers regular, frequently zygomorphic in consequence of oligomery in the gynæceum; sometimes actinomorphic (Fig. 312): stamens five, often connate at the base: ovary usually trilocular, with numerous ovules; placentation axile: fruit a capsule: seed with endosperm. Mostly herbs with milky latex.

The gynæceum is often oligomerous, and then usually trimerous (*e.g.* most species of Campanula and Phyteuma), sometimes bilocular (Jasione, species of Phyteuma): when isomerous, the carpels are either antisepalous and therefore opposite to the stamens (*e.g.* a few species of Campanula, Fig. 312, Michauxia, Wahlenbergia), or antipetalous and therefore alternate with the stamens (*e.g.* Musschia, Platycodon).

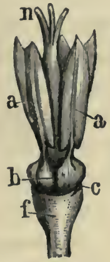

FIG. 456.—Andrœcium and gynæceum of Campanula: *f* inferior ovary; *c* insertion of the corolla; *a* anthers; *b* expanded base of the stamens; *n* stigmata (mag.).

FIG. 457.—*A* Floral diagram of a species of Campanula with a trimerous ovary (*e.g. C. persicifolia*): *a* gynæceum of Lobelia.

Campanula rotundifolia, the Hare-bell, *glomerata*, and other species are common in fields, on heaths, etc., etc.: *C. Medium* is the Canterbury-bell cultivated in gardens. *Phyteuma orbiculare* and *spicatum*, the Rampions, are indigenous in parts of England; the flowers are in capitula, and the calyx is deeply 5 cleft with spreading teeth: nearly allied is the genus Jasione; *J. montana*, the Sheep's-bit, is common in England. Specularia has a rotate corolla; *S. Speculum*, Venus's Looking-glass, is cultivated.

Order 2. LOBELIACEÆ. Flowers dorsiventral, resupinate (Fig. 458; see p. 511): the corolla commonly forms a tube which is more or less cleft on one side, and the limb is divided into two lips, the lower one consisting of three lobes (Fig. 458 *A*, *u*), and the upper of two smaller ones (*A*, *o*): at their first formation the position of these parts is exactly the reverse, but in the course of development the pedicel undergoes torsion, so that those parts which are originally posterior become anterior, and *vice versâ*: anthers syngenesious (Fig. 458 *B*, *sr*) and unequal in consequence of the dorsiventrality of the flower: ovary 1-, 2-, or 3-locu-

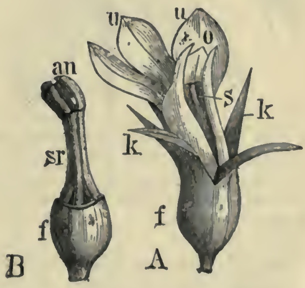

FIG. 458.—*A* Flower of Lobelia: *f* ovary; *k* calyx; *o* upper, *u* under lip of the corolla; *s* stamens. *B* Andrœcium and gynæceum of the same: *sr* tube formed by the stamens; *an* anthers (mag.).

lar, with numerous anatropous ovules : fruit a capsule : seed with endosperm. Herbs or shrubs usually with milky latex.

L. Dortmanni, the Water Lobelia, and *L. urens*, the acrid Lobelia, occur in some parts of England.

Cohort II. **Rubiales.** Flowers generally regular, actinomorphic or zygomorphic : calyx generally present : stamens epipetalous : gynæceum 2–5-merous : ovary uni- or multi-locular : ovules 2—∞ : leaves generally opposite.

Order 1. RUBIACEÆ. Flowers regular, 4- or 5-merous : calyx leafy or suppressed : corolla with valvate æstivation : ovary 1- or 2-locular, consisting of 2 carpels, 1- or many-seeded : seed usually containing endosperm : leaves decussate, stipulate : stipules (see p. 48) often similar to the true leaves (Fig. 459 *A*, *n n*) : the true leaves are distinguished by the branches which arise in their axils (Fig. 459*A*, *f f*, *s s*).

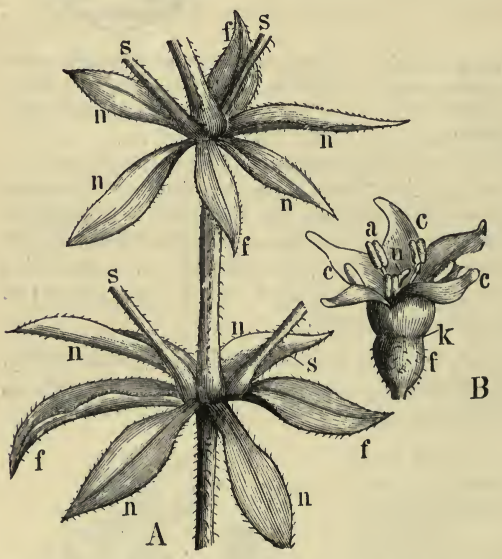

FIG. 459.—*A* Portion of a stem of *Rubia Tinctorum* : *ff* the decussate leaves with the young shoots (*s s*) in their axils ; *n n* the free stipules resembling the leaves (nat. size). *B* Flower (mag.): *f* ovary ; *k* calyx (rudimentary) ; *c* corolla ; *a* anthers ; *n* stigma.

Sub-order 1. STELLATÆ. Stipules large and leafy : loculi 1-seeded.

Galium, Bedstraw, has a rotate 4-lobed corolla and an inconspicuous calyx, usually tetramerous: *G. verum*, *Mollugo*, *Aparine*, and others are common in hedges and pastures. Asperula has an infundibuliform corolla, but in other respects the flower resembles that of Galium ; *A. odorata*, the Wood-ruff, is common : *A. cynanchica* is the Squinancy-wort. *Rubia Tinctorum*, the Dyer's Madder, has a pentamerous flower, a rotate 5-lobed corolla, and a baccate fruit ; it is used in dyeing and largely cultivated ; it is indigenous in Southern Europe and the East ; it is closely allied to the British species *R. peregrina*, the Wild Madder. Sherardia has a tubular 4-lobed corolla, and a conspicuous calyx with a 4–6 toothed limb which persists on the top of the fruit; *S. arvensis*, the Field Madder, is found in cultivated and waste places.

Sub-order 2. Coffeeæ. Stipules scaly: loculi 1-seeded.

Coffea arabica, the Coffee-tree of Africa, is grown in the tropics; the fruit, a berry, contains one or two seeds; the so-called coffee-bean is the seed, which consists of hard endosperm and contains a small embryo. Cephaelis yields Ipecachuana.

Sub-order 3. Cinchoneæ. Stipules scaly; loculi many-seeded.

Various species of Cinchona, indigenous to the eastern slopes of the Andes, but cultivated in Java and the East Indies, yield the cinchona-bark from which Quinine is prepared. Bouvardias are ornamental greenhouse plants from Central America.

Order 2. Caprifoliaceæ. Flowers usually pentamerous, actinomorphic or zygomorphic: corolla usually with imbricate æstivation; gynæceum 2–5-merous: ovules suspended: fruit baccate; seed with endosperm: leaves opposite, usually exstipulate. Mostly trees or shrubs.

Fig. 460.—Floral diagram of Caprifoliaceæ. *A* Leycesteria: *a* gynæceum of Lonicera; *b* of Symphoricarpus.

Fig. 461.—Flower of *Lonicera Caprifolium*: *f* ovary; *k* calyx; *r* corolla-tube; *c c* the five lobes of the limb; *st* stamens; *g* style; *n* stigma.

Tribe 1. *Sambuceæ.* Flower regular, sometimes completely actinomorphic, corolla rotate (Fig. 329 *C*): one ovule in each loculus.

Sambucus has a 5-partite corolla, and 3–5 seeds in the berry; *S. nigra* is the Elder; *S. Ebulus* is the Dwarf Elder or Danewort. Viburnum has a 5-partite corolla, and one seed in the trimerous berry, two carpels being abortive; *V. Lantana* and *V. Opulus*, the Guelder Rose, are common; a form of the last species is cultivated in which all the flowers (and not merely those at the circumference of the corymb as in the original species) have a large corolla, and are barren; *V. Tinus* is the Laurustinus. *Adoxa moschatellina*, the Moschatel, is a small plant occurring in damp woods; its flowers are 4- or 5-merous; it appears that there is no calyx, that which is regarded as the calyx being probably an involucre of bracteoles and bract: the stamens are each divided into two, so that there are 8–10 bilocular anthers.

Tribe 2. *Lonicereæ.* Flowers more or less irregular, zygomorphic; corolla tubular: loculi containing several ovules.

Lonicera, the Honeysuckle, has a somewhat bilabiate corolla (Fig. 461), and a 2–3-locular ovary; *L. Caprifolium* and *Periclymenum*, with a climbing stem, are well-known garden shrubs; in many species the fruit of two adjacent flowers grow together to form a single berry (*e.g. L. alpigena*). *Symphoricarpus racemosus*, the Snowberry, has a 4–5-locular ovary with white berries; it is a common ornamental shrub. Diervilla (or Weigelia) has a bilocular capsule; *D. florida* and *rosea* are ornamental shrubs. *Linnæa borealis* is a small creeping plant in Scotland; it has 4 unequal stamens, the posterior being suppressed, and a trilocular ovary.

Cohort III. **Asterales.** Flower either irregular or regular, pentamerous, zygomorphic in consequence of oligomery in the gynæceum: calyx inconspicuous, often wanting: stamens epipetalous, alternating with the segments of the corolla: ovary unilocular, ovule solitary.

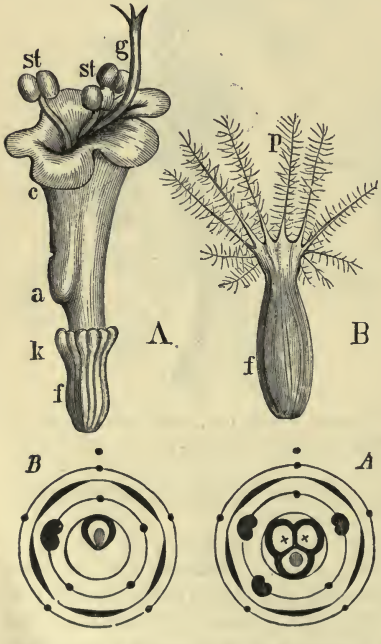

FIG. 462.—*A* Flower, *B* Fruit of Valerian: *f* ovary; *k* calyx; *c* corolla; *a* spur: *st* stamens; *g* style; *p* pappus. Floral diagrams, *A* of Valerian; abortive carpels × ×: *B* of Centranthus.

Order 1. VALERIANACEÆ. Flower irregular: calyx rudimentary, sometimes eventually assuming the form of a hairy crown of ten rays, called a *pappus*, which is not developed until after flowering (Fig. 462 *B*, *p*); during flowering it remains short and infolded (Fig. 462 *A*, *k*): stamens 1–4, usually three: carpels three, of which, however, usually only one developes, so that the fruit is unilocular (Diagram *A*, Fig. 462); ovule single, suspended: seed without endosperm: leaves decussate, exstipulate.

Of the genera occurring in Britain, Valeriana and Centranthus have a pappus whilst Valerianella has not. *Valeriana officinalis*, and *dioica*, are common in damp places. Valerianella has a toothed calyx-limb; many species are common in fields: *Valerianella olitoria*, Corn-salad, or Lamb's-lettuce, is eaten. *Centranthus ruber* is an ornamental plant; only one stamen and one carpel are developed (Fig. 462, Diagram *B*); at the base of the tube of the corolla is a spur which is indicated in Valeriana by a protuberance.

Order 2. DIPSACEÆ. Flower more or less dorsiventral, surrounded by an epicalyx (Fig. 463 *k′*) formed of connate bracteoles: calyx often plumose or bristly (Fig. 463 *k*): corolla usually bilabiate: stamens only four, the posterior one being suppressed: ovary apparently dimerous, one carpel being more or less completely suppressed, unilocular, with one suspended ovule: seed with endosperm: leaves decussate, exstipulate: flowers in a dense capitulum surrounded by an involucre of bracts: the outer florets are usually ligulate: the receptacle may or may not bear scaly bracts (paleæ): fruit invested by the epicalyx which is cleft longitudinally.

Dipsacus, the Teazle, has a calyx without bristles; the capitula of *Dipsacus Fullonum* are used in finishing woollen cloth, for the sake of the strong hooked spines of the paleæ: *D. sylvestris* is common on waste ground. In the genus Scabiosa, the paleæ, which are usually present, are not spinous: in the sub-genus Asterocephalus, the epicalyx (or involucel) is 8-furrowed, and its projecting limb is dry and scarious; *S. Columbaria*, with a 5-lobed corolla, is common in dry pastures: in the sub-genus Succisa, the limb of the 8-furrowed epicalyx is herbaceous; *S. succisa*, with a 4-lobed corolla, occurs in damp meadows: in the sub-genus Knautia, there are no paleæ but the receptacle is hairy, and the epicalyx is 4-furrowed; *S. arvensis* is common in fields.

Order 3. COMPOSITÆ. The flowers are always collected into many-flowered capitula (sometimes only 1-flowered); different kinds of flowers (☿, ♀, or sterile) generally present in the same head: ovary dimerous unilocular, with a basal, erect, anatropous ovule: the calyx is rarely present in the form of small leaves or scales (Fig. 466 *D*, *p*); more commonly it is a crown of simple or branched hairs (pappus; Figs. 464 *p*; 466 *A*, *E*, *p*), and is not developed till after the flowering is over; sometimes the calyx is wholly wanting: corolla tubular, either regular, and 5-toothed (Figs. 464 *A*, *c*; 466 *C*, *m*, *c*), or irregular and expanded at the upper end in a lateral limb with 3 or 5 teeth (Figs. 464 *B*; 466 *B*, *ra*; 466 *A*, *ra*, *c*), when it is said to be *ligulate*: the stamens are short, inserted upon the corolla (Fig. 464 *A*, *st*); the anthers are elongated and syngenesious, forming a tube through which the style passes (Figs. 464 *A*, *a*; 466 *A*, *a*): this is bifid at its upper end (Fig. 464 *A*, *n*; 466 *A* and *C*, *n*): on each of these branches the stigmatic papillæ are arranged in two rows: in the wholly ♀ flowers the styles are usually shorter (Fig. 464 *B*, *g*): fruit a cypsela (p. 530), crowned by the pappus (Fig. 466 *A*, *E*, *D*, *p*) when it is present (Fig. 466 *F*, *f*): sometimes the fruit has its upper end prolonged into a beak, and its surface is covered with ridges or spines (Fig. 466 *E*): seed without endosperm.

Usually herbs with scattered (more rarely decussate), exstipulate leaves, often with milky latex. The capitula are always surrounded by a number of bracts forming an involucre (Fig. 466 *B*, *C*, *i*). The scaly bracts of the individual florets (paleæ) may be present or wanting (Fig. 466 *C*, *d*).

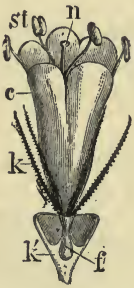

FIG. 463.—Flower of Scabiosa (mag.): *f* ovary; *k'* epicalyx (long sect.); *k* calyx; *c* corolla; *st* stamens; *n* stigma.

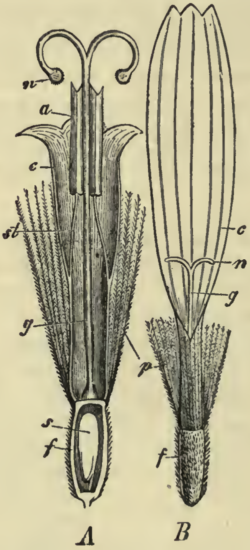

FIG. 464.—Flower of Arnica (mag.). *A* Tubular floret from the centre (disc) (longitudinal sect.). *B* Ligulate marginal floret (ray): *f* ovary; *p* pappus; *c* corolla; *a* anthers; *n* stigma; *g* style; *s* ovule.

FIG. 465.—Floral diagram of Compositæ (tubular floret).

The Compositæ are classified according to the form of the flowers and to the distribution of the different kinds of flowers in the inflorescence.

Sub-order I. TUBULIFLORÆ. The capitula either consists entirely of ☿ tubular florets (by tubular flowers are meant those with a regular 5-toothed corolla) or the central florets (florets of the disc) are tubular and ☿ (Fig. 464 *A*), whereas the florets of the ray are ligulate and ♀ or sterile, and form one or two rows (Figs. 464 *B*; 466 *B* and *C*, *ra*).

Tribe 1. *Eupatorieæ.* Leaves mostly opposite: flowers all tubular, ☿; the branches of style narrow; papillæ extending to the middle.

Eupatorium cannabinum, the Hemp Agrimony, is common in damp places.

Tribe 2. *Asteroideæ.* Leaves alternate: ray-florets ♀ or sterile, generally ligulate: branches of the style hairy above, papillæ extending to where the hairs begin. Many species of Aster, belonging chiefly to North America, are cultivated as ornamental plants, as also *Callistephus hortensis*, commonly known as the China Aster. *Erigeron acre*, *alpinum*, and *canadense* occur in England; the last is an imported weed. *Bellis perennis*, the Daisy, has no pappus. *Solidago virgaurea* is the Golden Rod.

FIG. 466.—Flowers of Compositæ: *f* fruit or ovary: *h* its beak; *p* pappus; *c* corolla; *s* stamens; *a* anthers; *n* stigmata. *A* Ligulate flower of Taraxacum, with a 5-toothed corolla-limb, ☿. *B* Capitulum of Achillea: *ra* floret of the ray, with ligulate 3-toothed corolla, ♀; *m* ☿ florets of the disc, with a 5-toothed tubular corolla; *i* involucre. *C* Longitudinal section more highly magnified; *r* receptacle; *i* involucre; *d* bracteoles (paleæ); *ra* floret of the ray; *m* florets of the disc; *n'* stigmata of the ♀ flowers. *D* Fruit of Tanacetum with a scaly pappus: *E* of Taraxacum, with a hairy pappus; *h* beak: *F* of Artemisia without a pappus (mag.).

Tribe 3. *Senecionideæ.* Leaves alternate: ray-florets in one row, ligulate ♀, rarely absent: branches of the style tufted at the tips.

Senecio vulgaris, the common Groundsel, has no ray-florets. *Arnica montana* occurs in Alpine woods. Two species of Doronicum (*D. Pardalianches* and *plantagineum*) have become naturalized in England. *Petasites vulgaris*, the

Butter-bur, and *Tussilago Farfara*, the common Coltsfoot, are common in damp fields.

Tribe 4. *Anthemideæ.* Leaves alternate: ray-florets ♀, ligulate or tubular: branches of style tufted at the tips: involucral bracts scarious: pappus 0, or minute.

Artemisia Absinthium, Wormwood, *A. vulgaris* and *campestris* are common: *Chrysanthemum Leucanthemum*, the Ox-eye Daisy, is common in fields: *Matricaria Chamomilla*, the Wild Chamomile, has a hollow conical receptacle destitute of paleæ: *Anthemis nobilis*, the Common Chamomile, has a receptacle bearing paleæ, as also *A. arvensis*, the Corn Chamomile: *Achillea Millefolium* is the Milfoil, or Yarrow: *Tanacetum vulgare* is the Tansy: *Diotis maritima* is the seaside Cotton-weed.

Tribe 5. *Helianthoideæ.* Leaves opposite: ray-florets 0 or ligulate, yellow, ♀ or sterile: branches of style as in Asteroideæ.

Bidens is common in wet places. Galinsoga is naturalized in England. *Helianthus annuus* is the Sunflower; oil is extracted from the seeds: the tubers of *H. tuberosus*, a West Indian species, are rich in inulin (p. 114), and serve as a vegetable (Jerusalem Artichoke). Species of Zinnia, Rudbeckia, Dahlia, and Coreopsis are cultivated.

Tribe 6. *Helenioideæ.* Resemble the Helianthoideæ, but the receptacle is without paleæ. Species of Helenium, Tagetes, Gaillardia, are commonly cultivated as garden flowers.

Tribe 7. *Inuloideæ.* Leaves alternate: ray-florets frequently ligulate, ♀, yellow: anthers appendiculate at base.

In Inula (*I. Helenium*, the Elecampane), Pulicaria (*P. dysenterica*, the Fleabane), and others, the ray-florets are ligulate; whereas, in other genera, Gnaphalium (the Cudweed), Filago, Antennaria, the ray-florets are filiform; Antennaria is diœcious.

Tribe 8. *Cynareæ.* Flowers all tubular, the outer ones sometimes ♀ or sterile: style thickened below the branches: anthers often appendiculate at base: leaves generally armed with spines, alternate.

Arctium Lappa (*A. majus*), the Burdock, is common by roadsides; the leaves of the involucre are hooked and spinous. *Carduus nutans* and *crispus* are common (true) Thistles; *Cnicus lanceolatus*, *palustris*, *pratensis* (Plume-thistles), are common in damp districts. *Carlina vulgaris* is the Carline-Thistle; the inner leaves of the involucre, which are white, fold over the flower-head under the influence of moisture, but in drought spread widely open. *Onopordon Acanthium* is the Scotch or Cotton Thistle. *Centaurea Scabiosa* and *nigra*, the Knapweeds, are common everywhere: *C. Cyanus* is the Corn-flower or Bluebottle, occurring in wheat-fields. *Cynara Scolymus* is the Artichoke; the flower-buds are eaten as a vegetable. *Carthamus tinctoria*, the Safflower, is used in dyeing, In Echinops, the Globe-Thistle, numerous one-flowered capitula are collected into one large spherical head. Saussurea and Serratula are the Saw-worts.

Tribe 9. *Calenduleæ.* Ray-florets ♀ and usually ligulate: disc-florets usually sterile.

Calendula officinalis, the Pot Marigold, is a familiar garden plant.

Sub-order II. LABIATIFLORÆ. The ☿ disc-florets have a regular or a bilabiate corolla; the ray-florets have usually a bilabiate corolla.

Tribe 10. *Mutisieæ.* This tribe includes all the Compositæ with a bilabiate corolla: they come mostly from South America. Mutisia is one of the few climbing genera: it climbs by means of leaf-tendrils.

Sub-order III. LIGULIFLORÆ. All the florets are ☿; limb of the corolla 5-toothed and ligulate (Fig. 466 *A*).

Tribe 11. *Cichorieæ.* Mostly herbs, all containing latex in laticiferous vessels (p. 142).

Taraxacum officinale, the Dandelion, is the commonest of wild flowers. *Lactuca sativa* is the Lettuce: *L. Scariola*, *virosa*, and others are common in waste places. *Scorzonera hispanica* is eaten as a vegetable. *Tragopogon porrifolius* is the Salsafy; *T. pratensis*, the Goat's-beard, is common. *Cichorium Intybus*, the Chicory, is found by roadsides; the roasted roots are mixed with Coffee: *C. Endivia* (Endive) is a vegetable. To this tribe belong also the British genera Hypochæris (Cat's-ear), Arnoseris (Lamb's Succory), Leontodon (Hawkbit), Hieracium (Hawkweed), Sonchus (Sow-Thistle), Crepis (Hawk's-beard), Lapsana (Nipplewort), Picris.

PART IV.

THE PHYSIOLOGY OF PLANTS.

§ 1. **Introductory.** The province of physiology is the study of those phenomena which, taken together, constitute the life of the plant; in other words, whilst morphology is concerned with what plants *are*, and histology with their structure, physiology deals with what they *do*. These phenomena may be classified, according to their nature, into *functions*, or different kinds of physiological work.

The body of the plant, whether it be unicellular or multicellular, is one physiological whole. In the lower and simpler plants the various functions are equally discharged by all parts of the body; but in more highly-organised plants the functions are distributed among the members and tissues, that is, there is physiological division of labour (see pp. 2, 92). In these higher plants each member, and each tissue, is adapted to the performance of one or more functions, and is the *organ* (p. 2) by which these special kinds of physiological work are done.

The performance of their functions by the organs of the plant is, however, materially affected by various external conditions. For instance, the activity of the assimilatory function of green leaves is altogether dependent upon exposure to light of adequate intensity. Hence the object of physiology is not only to distinguish and study the various functions, and to demonstrate the relation between them and the internal structure and the external form of the organs performing them, but also to determine what are the external conditions by which the performance of the various functions is affected, and the modes in which these conditions exert their influence.

CHAPTER I.

GENERAL PHYSIOLOGY.

§ 2. **The Functions.** In entering upon the analysis of the vital phenomena of plants, it must be clearly understood that these phenomena all depend upon the living protoplasm; that the vital functions are performed by the protoplasm, though the other cell-contents and the cell-walls are not without their physiological importance. With regard to the functions themselves, it is apparent, in the first place, that the outcome of the physiological activity of the plant is the maintenance of itself, and the production of new individuals resembling itself. Hence a distinction may at once be drawn between the *nutritive* and the *reproductive* properties of protoplasm. Moreover, during its life, the plant responds, in a more or less marked manner, to the action of external forces, such as light, gravity, etc. This is a manifestation of another property of the protoplasm, namely *irritability* or sensitiveness. Very commonly the response to the action of the external forces is of the nature of movement: but movements may be spontaneously performed by various parts in virtue of the *automatism* of the protoplasm: the motile property of protoplasm may be termed *motility.*

The nutritive property of protoplasm requires, however, further analysis. First, it is clear that nutrition necessarily depends upon the absorption of food from without; hence the plant is capable of performing the function of *absorption.* Secondly, from the food absorbed, protoplasm must ultimately be formed; the building up of protoplasm out of the food is termed *assimilation*, and the property by means of which this function is performed is termed the *metabolic* property of protoplasm.

But the metabolic processes going on in the protoplasm are not only such as lead to its maintenance or increase in bulk; on the contrary, the protoplasm is continually undergoing decomposition.

Stating these points in a more general form, it is to be clearly apprehended that there are two sets of chemical processes continually and simultaneously going on in living protoplasm. Of these, which together constitute the *metabolism* of the plant, one set includes those processes which lead to the formation of more complex substances from simpler ones; the other, those processes which lead to the formation of simpler substances by the decomposition of more complex ones. The former are designated the *constructive metabolism* or more shortly, the *anabolism*, of the protoplasm; the latter are designated the *destructive metabolism*, or the *catabolism*, of the protoplasm. It must also be clearly understood that these two sets of processes affect not only the state of the matter or substance of which the plant consists, but also the state of the energy in the plant: for the anabolism is accompanied by a conversion of kinetic into potential or latent energy, and the catabolism, by a conversion of potential into kinetic energy.

These various points will now be severally considered.

1. Absorption. The main idea connected with this function is the taking up of water and other substances into the plant from without; but it must not be overlooked that, in a multicellular plant, the cells absorb from each other.

In any case, the function of absorption depends upon the physical process of diffusion through membrane of substances in solution, or *osmosis.* For instance, supposing two adjacent cells; one of which has its cell-sap charged with sugar, whereas that of the other has none; the sugar will diffuse through the intervening cell-wall until the sap in both cells holds the same proportion in solution. This being the mode of absorption, it is clear that the substances can only be absorbed in the fluid form, either as liquids or gases.

So far the function of absorption would appear to be a simply physical process. It must, however, be borne in mind that the cell-wall is lined by living protoplasm, which modifies the purely physical diffusion through the cell-wall, both as regards the nature and relative quantity of the substances which pass into or out of the cell; so that the physical laws of osmosis, as determined by experiments with dead membrane, are not directly applicable to the osmotic phenomena of a living cell.

There is one manifestation of the osmotic properties of living plant-cells which is of such fundamental importance, particularly in connexion with movement, that it requires special mention. It is this, that the cells tend to take up such large quantities of water, that a considerable pressure is set up in the cell between the cell-sap, on the one hand, and the elastic cell-wall on the other. This state of tension is known as *turgidity* or *turgescence*, and a cell in this state is said to be *turgid.* The conditions upon which turgidity depends are three: first, the presence of osmotically active substances in the cell-sap to attract water; second, the presence of a layer of protoplasm lining the cell-wall; third, the presence of an elastic cell-wall. With regard to the first of these conditions, the necessity for it is obvious. It appears that the osmotically active substances in question are especially the organic acids or acid salts, which are abundantly produced in the metabolism of plants. The significance of the second condition is, that the layer of protoplasm prevents, at least within certain limits, the escape of the cell-sap as the pressure in the cell increases, and it is on this account that the high degree of turgidity of plant-cells is attained. Finally, the presence of an elastic cell-wall is obviously a necessary factor, for without resistance there can be no pressure.

It commonly happens, as will be subsequently pointed out in many instances, that an escape of cell-sap from turgid cells may take place without any rupture or injury of the cells; this is termed the escape of cell-sap by *filtration under pressure.*

It is clear, since the plant can only absorb dilute solutions of solids dissolved in water, that a much larger quantity of water than is necessary for the immediate wants of the plant, must be absorbed; and it is necessary that this excess of water should be got rid of. It is got rid of mainly in the form of watery vapour which is exhaled into the air. This exhalation of watery vapour is not simply physical evaporation, but is a vital phenomenon controlled by the living protoplasm; it is termed *transpiration.*

2. METABOLISM. This term refers to all the chemical changes which go on in living protoplasm itself, and which it induces in other substances.

a. Anabolism. It has been already stated that the metabolic processes included under this head, are those in which complex substances are formed from simpler ones. The most complex substance of all being protoplasm, it may be stated that the end of the anabolic processes is the construction of protoplasm.

The anabolic process which is most fundamentally important, and which is most characteristic of plants as opposed to animals, is the construction, by the green parts of plants under the influence of light, of organic substance from carbon dioxide absorbed from the air, and water absorbed from the soil. This is the first step in the process of assimilation as carried on in plants containing chlorophyll.

b. Catabolism. Under this head are included the dissociations which the molecules of protoplasm undergo, and those which it induces in other complex substances, either directly, or by means of certain metabolic substances known as *enzymes* or *unorganised ferments.*

In most cases the catabolism of the plant is accompanied by a gaseous interchange between the plant and the air, of this nature that the plant absorbs oxygen gas and gives off carbon dioxide. This gaseous interchange is known as *respiration.*

The *Products of Metabolism* may be classified as *plastic products* and *waste-products*: the former are such as can be further worked up in anabolism; the latter are not so used, but are withdrawn from the sphere of the metabolic activity, by being either excreted, or secreted in the insoluble form in special receptacles (see pp. 137 ff). Of the products of catabolism, carbon dioxide is the most constant.

3. IRRITABILITY. It is in virtue of the irritability of its protoplasm that the plant is in relation with the external conditions under which it is living. Any sudden change in the external conditions, or in the direction or intensity of the forces acting upon the plant, evokes some more or less evident response; that is, it acts as a *stimulus*, inducing a more or less sudden evolution of kinetic energy. The most striking response to the action of a stimulus is the performance of a movement: it must not, however, be inferred that because stimulation may fail to produce a responsive movement of any part, the protoplasm of that part is not irritable; for it must be borne in mind that the mechanical conditions may be such as to render movement impossible.

That it is essentially the protoplasm which is the seat of irritability is shown by the fact that naked masses of protoplasm, such as zoospores and the plasmodia of Myxomycetes, are highly irritable.

4. AUTOMATISM. Movements may, however, take place without the action of a stimulus, such movements being distinguished as *spontaneous* or *automatic*. They are to be ascribed to spontaneous evolutions of energy in the plant, which may be sudden or periodic.

5. MOTILITY. This property, by means of which the movements, whether spontaneous or induced by stimuli, of parts of plants are performed, resides, like the irritability, in the protoplasm, as is clearly shown by the movements of naked masses of protoplasm.

6. REPRODUCTION. The function of reproduction consists essentially in the throwing off by the individual of portions of its protoplasm, by which new individuals resembling itself are produced. The reproductive property is generally widely distributed in plants, so that almost any part, if cut off, can develope the missing members, thus completing its segmentation and producing a new individual. In most cases, however, there is provision for the formation of special reproductive cells, termed

generally *spores*, each of which is capable of developing into a new organism (see pp. 3, 67).

§ 3. **The External Conditions.** The functions of the plant can only be carried on under a certain coincidence of favourable external conditions. Thus, an ordinary green plant will only flourish when the conditions are such that it is supplied with appropriate food, with water, and with oxygen for its respiration, and is exposed to a suitable temperature and to sufficiently intense light.

The importance of a supply of food and of water is sufficiently obvious to need no further explanation here. The importance of a supply of oxygen is that without it the normal catabolic processes which are attended by an evolution of kinetic energy in the plant would either cease, or be so far suppressed that the plant would no longer manifest its vital phenomena; for instance, it would cease to grow, and would eventually die. But it must not be assumed that these catabolic processes are the ultimate source of energy in the plant: on the contrary, the energy evolved in the decomposition of a substance only represents a part or the whole, according to the degree to which decomposition proceeds, of the energy expended in producing the substance. And here it is that the importance of heat and light to the plant becomes apparent; for the heat and light of the sun are the ultimate sources from which the plant obtains the energy necessary for the maintenance of its life. Heat is an essential condition to the performance of all the vital functions of the plant: and light is an essential factor in that most fundamental of all the nutritive processes of the green plant, the assimilation of carbon dioxide.

Inasmuch as the influence of heat and light is so comprehensive, it may be generally considered now, the detailed consideration of these and other external conditions being relegated to the discussion of the functions which they especially affect.

HEAT. Every function of the plant can only take place within certain limits of temperature: that is, between a certain *minimum* and a certain *maximum* degree. Between these limits there is for each function a degree of temperature, the *optimum*, at which that function is carried on with the greatest activity; any fall of temperature from this optimum, or any rise above it, leads to a diminished activity of the function. These general laws have been arrived at by observation of such processes as movement, absorption by the roots, assimilation, etc.

It may be stated generally that all the functions of plants inhabiting temperate climates begin to be carried on at a temperature a few degrees above the freezing-point; as the temperature rises to 25°–30° C. the activity of the functions is increased and the optimum attained; with a further rise the activity of the functions is diminished, and at 45°–50° C. they commonly cease altogether. In the case of plants which naturally grow in warmer climates, the minimum-temperature is somewhat higher than that stated above. Thus a pumpkin-seed will not germinate at a temperature below 13° C.

The power of withstanding the injurious effect of exposure to too high a temperature depends mainly upon the proportion of water which the plant, or any particular part of it, contains. Thus, dry peas can withstand exposure for an hour to any temperature up to 70° C., whereas, when they have been soaked in water, exposure to a temperature of 54° C. proves fatal. Most parts of plants are killed by prolonged exposure to a temperature, in air, of about 50° C., and in water, of about 45° C.

Injury or death by exposure to cold, is only induced when the temperature falls—in some cases many degrees—below freezing-point. Some plants—just those, namely, such as Lichens, and some Fungi and Mosses, which can undergo desiccation without injury—are not killed by exposure to low temperature. Here, also, the liability to injury depends upon the amount of water contained in the tissue. Thus, dry seeds and the winter-buds of trees can readily withstand low temperatures; but when they contain a considerable quantity of water, as when the seeds are germinating or the buds unfolding, they are very susceptible to injury. When a part of a plant, which contains a large proportion of water, is exposed to a low temperature, a portion of the water contained in the cells escapes from them and becomes frozen on their surface, the whole tissue at the same time contracting; the water does not freeze in the interior of the cells. The water which has

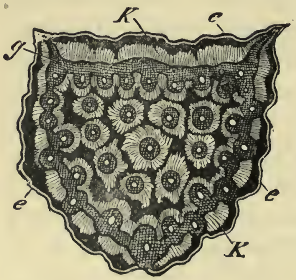

FIG. 467.—Transverse section of a frozen leaf-stalk of *Cynara Scolymus*: *e* the detached epidermis; *g* the parenchyma in which lie the transverse sections of the vascular bundles (left white); *K K* the incrustation of ice consisting of densely-crowded prisms (the cavities of the ruptured tissue are left black in the figure).

thus escaped and frozen forms an incrustation (Fig. 467), consisting of a number of elongated ice-crystals arranged side by side. This ice is very pure, for the substances in solution in the cell-sap remain behind in a more concentrated form.

It has been ascertained that this formation of ice is, in itself, not necessarily fatal in all cases. If the frozen part be slowly thawed, the cells may gradually reabsorb the water, and so return to their previous normal condition. If, however, the frozen part be rapidly thawed, the cells cannot absorb the water sufficiently rapidly; it therefore either collects in the intercellular spaces, causing discolouration and decay, or it runs off and evaporates, so that the part dries up. In many cases, however, slow thawing does not ensure immunity; for instance, the leaves of the Pumpkin or the Dahlia: it appears that, in such cases, the escape of water from the cell, which takes place at the time of freezing, causes fatal disorganisation of the cells. Again, in the case of long-continued cold, the ice formed outside the cells may be gradually removed by evaporation, so that on thawing, the water necessary to restore the normal condition of the cells is not forthcoming.

The effect on the trunks of trees of exposure to cold is to cause radial splits, which close up again as the temperature rises, but which actually heal only in the cortex. The splitting is due to the unequal contraction of the wood, which is greater in the external more watery portion, than in the interior.

LIGHT. The influence of light may be considered under two heads: (1) the *chemical effects*, produced for the most part by the less refrangible rays of the spectrum; (2) the *mechanical effects*, produced mainly by the highly refrangible rays.

The most conspicuous *chemical effects* are manifested in plants which normally contain chlorophyll. They are:—

a. The formation of chlorophyll: in Phanerogams the colouring-matter of the chloroplastids cannot acquire its green hue (except in the seedlings of Conifers and some other plants), but remains yellow (etiolin), unless exposed to light of not too great intensity. This effect is not confined to the rays of low refrangibility, but is produced (with equal intensity of light) also by those of high refrangibility. The formation of chlorophyll is also dependent on temperature, and will not take place if it be too low; hence the shoots of plants developed in the early spring remain yellow if the weather is cold.

b. The *assimilation of carbon dioxide* by the chloroplastids will only take place in the presence of light of considerable intensity; it is especially a function of the rays of low refrangibility, as will be subsequently explained. This is also true of the first steps in the assimilation of mineral nitrogenous food (nitrates).

The most conspicuous *mechanical effects*, exhibited by plants of all kinds are:—

a. The paratonic effect. All parts of plants grow more rapidly in feeble than in strong light, as is shown by the excessive length attained by the shoots of plants grown in the dark; hence, light exercises a retarding influence on the rate of growth; it likewise inhibits the spontaneous movements of motile leaves.

b. The phototonic effect. Dorsiventral leaves, when growing, generally cease to grow, and when motile, lose the power of movement, if long kept in darkness; but they soon regain the power of movement on being again exposed to light; this condition of motility induced by light is known as *phototonus*.

c. The directive effect. The direction of the incident rays of light affects the position of growing and other motile members: these phenomena are designated by the general term *heliotropism*.

The various influences of light are well illustrated by plants grown in darkness, or *etiolated* plants. For instance, an etiolated potato-shoot has a stem with excessively long internodes, a result of the absence of the paratonic effect of light; very small leaves, in consequence of the absence of the phototonic effect; no chlorophyll, in consequence of the absence of the chemical action of light. Etiolation can, however, be induced, not only in plants which normally possess chlorophyll, but in others as well; for instance, Fungi grown in darkness exhibit the characteristic excessive elongation. Again, plants grown in light of low refrangibility (yellow or red) show the elongation characteristic of etiolation; chlorophyll is formed, and the leaves are fairly well developed, but there is no heliotropic curvature: grown in light of high refrangibility (blue), the stem is stunted and the leaves very small, though chlorophyll is developed, and heliotropic curvature is well marked; they soon die.

§ 4. **The Functions of the Tissues.** In dealing with this subject, it is important to distinguish between the *vital* and the *physical* functions; to distinguish, that is, the functions which depend upon the activity of the living protoplasm, from those which depend upon some chemical or mechanical property of the cell-sap, or of the cell-wall, of the constituent cells. The following remarks apply especially to the terrestrial higher plants.

a. The Tegumentary Tissue (see pp. 132, 153), whether primary (epidermis) or secondary (periderm), has as its primary function the mechanical protection of the underlying tissues: but it has the further functions of absorption and of preventing excessive transpiration.

The absorptive function is confined to the primary tegumentary tissue: it is by means of this tissue that absorption is carried on by subterranean roots, either with or without root-hairs (see pp. 154, 159), as also by the general surface of submerged parts of aquatic plants (p. 157).

The prevention of excessive transpiration is effected by the more or less well-marked cuticularisation of the walls of the epidermal and peridermal cells of sub-aerial parts. Since these walls, though more or less pervious to gases, are almost or altogether impervious to watery vapour, the watery vapour evolved in the interior of the plant has to escape through special apertures, namely the stomata and the lenticels: and the transpiration is further regulated (see p. 156) by the opening and closing of the stomata. The importance of the tegumentary tissue in preventing desiccation is directly established by the fact that parts of plants deprived of their tegumentary tissue quickly dry up: and indirectly, by the relation between the degree of development of this tissue and the conditions of life of the plant. Thus, this tissue is highly developed in plants which grow in dry situations, whereas in the submerged parts of aquatic plants it is imperfectly differentiated, and there are usually no stomata or lenticels: hence, the more the conditions of life tend to promote transpiration, the more highly-developed is the tegumentary tissue.

The epidermis of sub-aerial parts also produces hairs of various kinds. The function of these is often secretory, indicating the importance of the epidermis as a glandular tissue (see p. 142). But, more commonly, they are purely protective, serving to diminish transpiration and radiation, and to screen the chlorophyll from too intense light. A clothing of hairs is characteristic of *xerophilous* plants; plants, that is, which habitually grow in dry soil and sunny situations.

The primary tegumentary tissue is also of importance in connection with reproduction, as it sometimes gives rise to reproductive organs (*e.g.* sporangia of Leptosporangiate Filicinæ).

b. The Parenchymatous Tissue (see p. 131), consisting as it typically does of cells which contain living protoplasm, is the seat, not only of the metabolic processes, but also of the movements and irritability of plants.

Different nutritive functions are discharged by various regions of this tissue. For instance, the parenchymatous tissue of sub-aerial parts, lying near the surface and exposed to light, contains chlorophyll, and carries on the assimilation of carbon: this applies especially to the leaves. Again, the cells of this tissue are frequently glandular (see p. 137), containing or excreting various waste-products: or they serve as depositories of reserve plastic substances (*e.g.* starch, etc.), or as conducting-tissue for organic substances.

It may also be pointed out that this tissue is connected with the reproductive processes in that the reproductive organs (*e.g.* hypodermal archesporium of most plants) are developed from it in part.

Further, the cells of this tissue, having usually extensible walls, are capable of being turgid and of varying in bulk: hence they are the seat of the movements of those members, or parts of them, in which movement is a mechanical possibility; and when turgid, they give a considerable degree of rigidity to the member of which they form part.

The intercellular spaces of this tissue, which are especially large in submerged parts of aquatic plants, are of great importance in connexion with transpiration and the distribution of gases in the plant: they communicate with the exterior by means of the stomata and the lenticels.

c. The Sclerenchymatous Tissue (see p. 132), more especially the prosenchymatous or fibrous form of it, has the purely mechanical function of giving firmness to the members in which it is present. Whilst it is true that a considerable degree of rigidity is afforded by turgid parenchymatous tissue, and that many members containing little or no sclerenchymatous tissue can grow erect (*e.g.* gonidiophores of moulds, and succulent stems of herbaceous annuals), yet this source of rigidity is precarious, as it is so largely dependent upon external conditions, and is therefore insufficient in the case of perennial plants. In these plants rigid tissue (stereom; see p. 133) is developed, and it is distributed in the body in just such a manner as most adequately meets the mechanical requirements in each particular case (p. 170). Stereom is most perfectly developed in the stems of land-plants which grow erect and have to support the weight of many leaves and branches: whereas in water-plants the development of stereom is rudimentary, for their stems, being supported by the water, do not need to be highly rigid.

When it is developed in the walls of fruits or in the seed-coats, the sclerenchymatous tissue serves to protect the seed from being eaten or digested by animals.

d. The Tracheal Tissue of the Xylem (see p. 133). It is clear that when a plant-body is massive, partly subterranean and partly subaerial, there must be some means for readily distributing the water and other substances absorbed by the root. This distribution may take place by diffusion from cell to cell; and, as a matter of fact, this mode of distribution suffices in some plants in which the seat of absorption is not far from that of consumption (*e.g.* larger Fungi and Algæ). But when these points are widely separated, special conducting-tissue, in the form of the tracheal tissue of the xylem, is differentiated.

The function of this tracheal tissue is demonstrated by the following experiment. If a cut be made all round the stem of a dicotyledonous tree, to such a depth as to penetrate far into the xylem, the effect is that the leaves borne on the stem and its branches above the incision will soon droop and wither. This is due to loss of water, in consequence of which the cells of the leaves lose their turgidity, and the leaf-blades and petioles are no longer sufficiently rigid to maintain their position of expansion. The loss of water is the result of the continuance of transpiration in the absence of a supply of water to meet it. The incision which has destroyed the continuity of the wood has also cut off the supply of water from the root. The relation between the development of the xylem and the activity of transpiration is well illustrated by the comparison of the vascular bundles of a land-plant with those of an allied submerged aquatic species. The former transpires actively and has well-developed xylem: the latter does not transpire at all, and has quite rudimentary xylem.

Conduction takes place in dicotyledonous tree-trunks only through so much of the peripheral portion of the wood as includes living parenchymatous cells. The thickness of this conducting region varies widely; it is relatively small where the wood is sharply differentiated into alburnum and duramen (see p. 199), and in such trees (*e.g.* Oak) section of the alburnum is soon followed by the withering of the leaves above the wound; it is more considerable in trees like the Beech, in which the transition from alburnum to duramen is gradual; and it is most extensive in those, such as Birch and Maple, in which there is no differentiation of alburnum and duramen. The dead portion of the wood does not conduct, but at most only serves as a reservoir of water.

The tracheal tissue of the xylem discharges a purely mechanical function in connexion with the conduction of water; it is incapable of any vital action inasmuch as it contains no protoplasm.

A fundamental anatomical fact connected with the conduction of liquids by the wood is that the functional tracheal tissue is destitute of intercellular spaces, and is, in fact, shut off from all communication with the external air. This occlusion is ensured, generally speaking, by the endodermis (p. 165); but in stems and roots which have grown in thickness, and in which the endodermis has been disorganised or thrown off, the compact bast-tissue replaces it functionally.

The liquid conducted from the roots to the leaves by the tracheal tissue is not pure water, but holds in solution substances absorbed by the roots from the soil; hence this tissue plays an important part in the distribution of food-materials in the plant.

e. The Sieve-Tissue (see p. 135). The function of the sieve-tubes or phloem-vessels is to convey proteids from the organs in which these substances are deposited or are being formed, to other parts in which they are either being consumed or deposited as reserve plastic material. This is demonstrated by the following experiment:—If a ring of tissue, extending inwards as far as the cambium, be removed from the trunk of a young dicotyledonous tree, the sieve-tubes will all be cut through, and their continuity interrupted. The effect of this upon the tree is that the portion of the trunk below the wound, and the roots, cease to grow and slowly die, whereas the trunk and branches above the wound remain healthy and continue to grow until the roots are no longer able to absorb water, etc., from the soil with sufficient activity. Inasmuch as the cortical tissue, through which the sugar travels, is necessarily also cut through, the operation deprives the lower parts of the body of the whole of their supply of organic plastic material from the leaves, but does not interfere with the conduction of water from the roots to the leaves.

The sieve-tubes differ from the vessels of the xylem in that they contain living protoplasm; their function is therefore probably not purely mechanical, but it is vital, though the relation of the protoplasm to the conduction of proteids in the sieve-tubes is not clear.

The companion-cells, and in their absence the cells of the bast-parenchyma (p. 180), which abut on the sieve-tubes, apparently serve in the leaves as the means by which the nitrogenous products of anabolism are brought to the sieve-tubes, and in other parts as the means by which the proteids of the sieve-tubes are distributed to the adjacent tissues; there is some evidence to show that these cells themselves actually carry on the formation of the proteids which form the characteristic contents of the sieve-tubes.

In certain cases (*e.g. Mimosa pudica*) some of the parenchymatous cells of the bast are specially modified apparently for the conduction of stimuli.

f. The Glandular Tissue. The essential function of the glandular tissue is to secrete, and the secreta are either plastic substances or waste-products.

It may be stated generally that the excretion of plastic substances on the surface of plants has special reference to their relation with insects. Thus, the excretion of sugar by floral nectaries is to attract insects to visit the flowers, and thus to ensure the advantages of cross-pollination at a certain, though relatively inconsiderable, cost. The excretion of sugar by extra-floral nectaries (p. 138) is an expense incurred by the plant with the object of attracting to it insects of a kind which will keep off noxious insects or other animals; these organs are especially characteristic of *myrmecophilous* (ant-loving) plants, which by this means provide themselves with a police of ants to keep off either other injurious (*e.g.* leaf-cutting) species of ants, or insects of other kinds (*e.g.* boring bees, etc.), or even herbivorous mammals. Perhaps the most remarkable instances of this kind is the production of small, solid, cellular "food-bodies" on the tips of the leaf-pinnules of a myrmecophilous species of Acacia (*A. sphærocephala*).

The secretion of waste-products has, as its immediate object, the removal of these substances from the sphere of metabolism; but their deposit at or near the surface serves the purpose of protection in various ways. For instance, the secretion of wax on the surface is an obvious protection against wet. Similarly there can be little doubt that when the system of resin-ducts, in plants which contain them (*e.g.* most Conifers, etc.), is opened by a wound, the resin serves to protect the raw surface both mechanically and antiseptically; and this doubtless also applies to the latex present in many plants. Further, these waste-products, by their bitter, acrid, or astringent taste, by their frequently poisonous properties (*e.g.* alkaloids), or by their hardness, serve to protect the plants from being eaten by animals; for instance, the presence of raphides, or of strongly acid sap, in the cells of leaves, etc., has been proved to protect them against the attacks of snails. The secretion of mucilage by the glandular hairs (colleters) often developed near the growing-points of stems and leaves, serves to keep the young tissues moist.

The special functional importance of the laticiferous tissue is not fully understood. There is no doubt that it is, in the first place, a reservoir of waste-products, since the latex generally consists largely of such substances (*e.g.* caoutchouc, as in *Siphonia elastica*; alkaloids, as in the opium of the Poppy, etc.). But the latex has also been found to contain plastic substances, such as proteids and carbohydrates, and in one case (the Papaw, see p. 627) a proteolytic ferment, and it has hence been inferred that this tissue may serve to conduct plastic substances throughout the plant; but this inference has not been satisfactorily established.

§ 5. **The Functions of the Members.** It has been pointed out (p. 6) that, in its highest development, the plant-body consists of the following members: root, stem, leaf. These members will now be considered from the physiological point of view.

a. THE ROOT. The most general of the functions of the root is that it absorbs the solid food of the plant in solution from the substratum, whatever it may be, on which the plant is growing; and that, at the same time, it acts as an organ of attachment: in submerged plants the latter is its main use.

In some few cases the plant is rootless (p. 63): under these circumstances other members become modified to perform the absorbent function of the root; in Salvinia, the aquatic leaves; in Psilotum, the subterranean shoots. In the "carnivorous" plants (*e.g.* Drosera, Dionæa, Nepenthes), though they possess roots, the leaves are adapted for the absorption of organic food in solution.

In a typical land-plant the development of the root-system is such as to ensure an adequate supply of food from the soil, and a supply of water sufficient to maintain the general turgidity of the plant in spite of continued loss of water by transpiration.

The root of such a plant is adapted for the performance of its functions both in its structure and in its properties. The most striking structural adaptation is that the walls of the superficial cells of the younger parts are not cuticularised, but remain pervious to water. Generally speaking, the absorbent area of the root is increased by branching; and, in many cases, also by the growing-out of the superficial cells of this region into root-hairs (see p. 159). It appears that the development of root-hairs is determined by the difficulty of obtaining water, on the one hand, and by the relative activity of transpiration on the other: thus root-hairs are usually not developed by aquatic plants, the roots of which, at least, are habitually immersed in water; nor by plants in which the transpiring surface is relatively small in proportion to the root-system (*e.g.* small-leaved Conifers; saprophytes, such

Fig. 468.—*A* Root-hairs (*h*) on the primary root (*w*) of a seedling, grown in water, of Buckwheat (*Polygonum Fagopyrum*); *hc* hypocotyl; *c* cotyledons. *B* (after Sachs) Ends of root-hairs showing their intimate connexion with particles of soil which adhere to the mucilaginous external layer of the cell-walls.

as Monotropa and Neottia). The root-hairs not only promote the absorption of water, but also the absorption of salts from the soil, coming, as they do, into very intimate relation with the minute particles of the soil. They thus give the root a firmer hold on the soil, and render it more serviceable as an organ of attachment.

Roots are capable of absorbing certain substances in the soil which are insoluble in water, or even in water holding carbon dioxide in solution. This is due to the fact that the absorbent cells (including root-hairs) contain acid sap, which saturates the walls, and can thus act upon substances with which the cells may be in contact.

The tegumentary tissue of aerial roots is specially modified in accordance with their external conditions. They have no root-hairs (except when they come into contact with a moist surface), but they have a more or less well-developed velamen (see p. 155), which serves as a means of absorbing water-vapour and gases from the air. Sometimes these roots contain chlorophyll, and act as assimilatory organs: this is also the case to a remarkable degree with the roots of the (aquatic) Podostemaceæ (see p. 63).

The primary internal structure of the root is remarkably constant through all the various groups of plants. It is always monostelic with the vascular bundles compacted into an axial cylinder (p. 171): between the axial cylinder and the epiblema is a considerable parenchymatous cortex, the cells of which take up from the absorbent cells the water and substances absorbed, and transfer them to the tracheal tissue of the bundles for conduction to the upper parts of the plant.

The growing-point is usually provided with a root-cap (pp. 61, 154) to protect it as it makes its way through the soil.

In many cases the root becomes adapted to serve as a depository of reserve plastic materials: such are the tuberous roots (p. 63) of various plants, in which secondary growth in thickness (see p. 105) produces a large amount of parenchymatous tissue, in the cells of which the plastic substances (starch, etc.) are deposited.

The physiological adaptation of the root is even more remarkable in its properties than in its structure, as is shown by its irritability to the action of various stimuli. Thus the action of the force of gravity causes roots (at least primary roots) to grow towards the centre of the earth (*positive geotropism*): the action of light, as a rule, causes the growing root to curve away from the source of light (*negative heliotropism*): a moist body causes the root to curve towards it (*positive hydrotropism*): contact with hard substances produces curvatures by which the direction of growth of the root is altered.

These various kinds of irritability are of great importance in ensuring the due performance of its functions by the subterranean root. Positive geotropism causes it to penetrate into the soil, and this is also promoted by negative heliotropism: positive hydrotropism causes it to grow towards the moister parts of the soil, and thus tends to ensure an adequate supply of water. Its sensitiveness to contact enables the root to get round obstacles which it may meet with in the soil. Similar phenomena of irritability are exhibited by aerial roots, but with various modifications in accordance with the widely different conditions.

b. THE STEM. The function of the stem is essentially this: to bear the foliage-leaves and the reproductive organs, and to bear them in such a way that they shall occupy the most favourable position for the performance of their respective functions. Further, it is the means of communication between the roots and the leaves. Occasionally it is specially modified to subserve other functions.

It has been already pointed out that the form of the stem varies widely in plants, and the most characteristic forms have been described (pp. 40, 44). The general physiological meaning of this variety of form is that different plants attain the most favourable position of their foliage-leaves and reproductive organs in different ways which depend upon the particular combination of external conditions under which they severally have existed.

The internal structure of the stem varies to some extent with its general habit, and mainly in the arrangement and relative degree of development of the sclerenchyma; thus, the sclerenchyma is more largely developed in an erect than in a trailing perennial stem.

The arrangement of the vascular tissue, however, depends essentially, at least in all those plants which have common bundles, upon the arrangement of the leaves. In stems having cauline bundles (p. 171) there is a more or less marked aggregation of the bundles towards the centre, so as to lead to the formation of an axial vascular cylinder, as in roots; this is especially marked in stems bearing small leaves, as in Lycopodium.

There is one point in connexion with the relation of the vascular tissue to the leaves which requires more special consideration. It has been pointed out (p. 191) that vascular tissue is formed secondarily in the stems (and roots) of most Dicotyledons and Gymnosperms, whereas it is not so formed in those of most Monocotyledons and Vascular Cryptogams. A consideration of the general habit of the plants in question at once affords a clue to this remarkable diversity. In the plants of the former groups, the stem, as a rule, branches considerably, and consequently there is every year an increase in the area of the leaf-surface of the plant; whereas in the plants of the latter groups, the stem branches but little if at all, and the area of leaf-surface remains approximately constant in the adult plant. It is clear that, in the former case, the increase of leaf-surface necessitates an increase in the conducting vascular tissue, a demand which is met by the annual formation of an ever-widening ring of vascular tissue by the cambium. Hence, in a plant of this kind, the vascular bundles in the leaves of any one year are continuous, in the stem, with the new vascular tissue formed in that year by the cambium.

Stems may be specially modified both in external form and internal structure for the performance of special functions. Thus in leafless plants the stem or its branches may become phylloid; that is, it may assume a flattened, leaf-like appearance (p. 44). The cortical ground-tissue of the stems of such plants resembles the mesophyll of foliage-leaves, not only in that the cells contain chlorophyll-corpuscles in abundance, but also in the more or less complete differentiation of a superficial palisade-layer from a more deeply placed spongy tissue. The reduction of the foliage-leaves and the compensating development of the stem is a characteristic of many xerophilous plants: under these circumstances the stem generally becomes succulent (as in Cactaceæ, p. 628, and some Euphorbiaceæ) owing to the development of a large amount of parenchymatous tissue.

Again, stems may be specially modified to serve as depositories of reserve materials (*e g.* tubers of potato), or of water (*e.g.* stems of Cactaceæ), when they are much thickened by the development of a large quantity of parenchymatous ground-tissue, in the cells of which the water or the reserve-materials are deposited. Or they may be developed into thorns (p. 44) as a protection against being eaten.

The special physiological properties of stems by which they assist in placing the foliage-leaves and reproductive organs in the most favourable position, are their various kinds of irritability to the action of external stimuli.

The physiological adaptation of stems is such that the movements which they perform in response to the action of external stimuli are always such as shall place the foliage-leaves and the reproductive organs in the most favourable position. Some stems, for instance, grow away from the centre of the earth (negative geotropism) and towards the light (positive heliotropism); these stems consequently grow up into the air, and take up such a position with regard to the direction of the incident rays of light that the leaves may be adequately exposed to them. Others, again, grow horizontally under the influence of gravity (diageotropism) and of light (diaheliotropism), and in this way spread out their leaves to the sun's rays.

In some cases stems which tend to grow erect into the air are unable to do so in consequence of being insufficiently rigid to maintain their own weight, and that of their leaves, etc. Such stems are enabled to obtain the necessary support by becoming attached to foreign bodies, such as other plants, rocks, etc. This attachment is sometimes purely accidental, as in the case of the *hook-climbers*, such as the Bramble, where the stem is covered with prickles which become fixed as the swaying shoot is blown about by the wind. But in other cases the attachment is the result of the mode of growth of the stem or its branches, in virtue of which they twine round any suitable foreign body with which they may come in contact. In some cases the stem and its branches are sensitive to contact, *e.g.* Dodder; in others, this sensitiveness is restricted to certain specially modified branches, termed tendrils (see p. 43, *e.g.* Vitis, Passiflora), and it is possessed by them in a very high degree.

c. THE LEAF. In the discussion of the morphology of the leaf it was pointed out that the forms of leaves are very various; so much so that it was necessary to classify them into a number of categories. Each of these will now be briefly considered with regard to its functions.

(1). *Foliage-leaves.* It may be stated generally with reference to land-plants, that the two great functions subserved by the leaf are, first, the construction of organic substance from the raw materials of the food; and second, the exhalation of watery vapour, or transpiration.

The internal structure of the leaf is in direct relation to these two functions (see p. 162). The particular significance of the form and arrangement of the cells of the mesophyll is made clear by the following considerations. The palisade-layers occur always, beneath the epidermis, at those surfaces which are directly exposed to the sun's rays. Further, if a plant which, when grown exposed to sunlight, has well-marked palisade-layers in its leaves, be grown in the shade, it will be found that the palisade-layers are imperfectly differentiated, even if they can be detected at all. The development of the palisade-layers is clearly a peculiarity of leaves which are exposed to sunlight. One explanation is this, that bright light not only promotes the assimilatory function, but also promotes the oxidation and decomposition of the chlorophyll. The palisade-tissue affords a means of protection from the latter effect. When a leaf-surface is exposed to diffuse daylight, the position of the chlorophyll-corpuscles in the palisade-cells is such as to expose them as fully as possible to the light; they are disposed on the surface-walls, both upper and lower, of the palisade-cells (*epistrophe*). When, however, diffuse daylight is replaced by direct sunlight, the position of the corpuscles is changed (see Fig. 469) so that their margin, and not their surface, is presented to the sun's rays; they are removed to the lateral walls and towards the inner end of the cell (*apostrophe*). It is clear that the elongated form of the cells facilitates this withdrawal of the corpuscles from too intense light, to light of a degree of intensity which promotes the assimilatory function to the utmost extent compatible with a due economy of the chlorophyll.

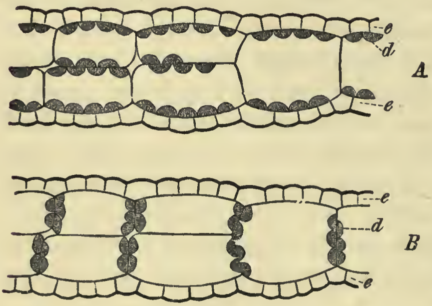

Fig. 469.—(After Stahl). Sections of the phylloid stem of *Lemna trisulca*, illustrating epistrophe and apostrophe of the chloroplastids: *A* position in diffuse daylight (epistrophe); *B* position in intense sunlight (apostrophe).

The spongy portion of the mesophyll is the tissue especially adapted to the transpiratory function. By means of the large intercellular spaces which form a system of channels throughout this tissue communicating with the external air by means of the stomata, a very large cell-surface, from which transpiration can readily take place, is brought into direct relation with the external air. Transpiration takes place from the cells of the spongy mesophyll into the intercellular spaces, and the watery vapour then escapes from the leaf by the stomata.

A brief consideration of the peculiarities of the leaves of aquatic plants will further establish these points. The characteristic feature of submerged leaves is that they are very much divided, and consequently present a relatively large surface by which they can absorb carbon dioxide and oxygen, as well as salts, from the water. The mesophyll of these leaves is not differentiated into palisade-tissue or spongy tissue; for, in the first place, the light to which these leaves are exposed is not intense, and, in the second, they do not transpire. A peculiar feature of these leaves is that the chlorophyll-corpuscles are contained principally in the epidermal cells. Floating leaves, on the other hand, usually have broad oval or rounded laminæ, a form which is evidently favourable to the retention of their position on the surface of the water. The epidermis of the upper surface is well-developed and possesses stomata; whereas the walls of the epidermal cells of the lower surface are thin and uncuticularised, so that they can absorb water and substances in solution, and there are no stomata. The mesophyll is differentiated into palisade and spongy tissue. The palisade-layers are arranged in the characteristic fashion towards the upper surface of the leaf; and commonly there lies between the superior epidermis and the palisade-tissue, a layer of aqueous tissue which serves to protect the chlorophyll of the latter from exposure to too intense light. Towards the lower surface, the mesophyll is channelled by large intercellular spaces, the use of which is to facilitate the aeration of the plant.

The foregoing consideration of the anatomy of these three types of foliage-leaves leads to the conclusion that the spongy tissue of the mesophyll is that in which both the assimilatory and the transpiratory processes can be most satisfactorily carried on; that, in fact, the amount of spongy mesophyll in a leaf may be taken as an indication of the degree of its physiological activity. Clearly the close arrangement of the cells in the palisade-tissue is not so favourable for the absorption of carbon dioxide or for the exhalation of watery vapour, as is the loose arrangement of the cells in the spongy tissue. The palisade-tissue is transpiratory and assimilatory tissue so adapted for action in intense light, that transpiration is diminished, and protection is afforded not only to the chlorophyll in its own cells, but also to that in the cells of the tissue which it covers.

In many xerophilous plants, more or less of the mesophyll may be destitute of chlorophyll, the cells containing much watery sap (see p. 164), so that the leaf serves as a reservoir of water.

Leaves are adapted not only structurally, but also by their irritabilities, to the performances of their functions. They are sensitive to the directive action of light and of gravity and, in the course of their growth they take up a definite position termed, on account of the predominating influence of light in determining it, the *fixed light-position.* The response of the dorsiventral leaf to the directive action of gravity, is generally one of *diageotropism*, that is it places its blade horizontal, with the ventral surface uppermost; and similarly, its response to light is to expose the upper surface of its blade at right angles to the direction of the incident rays (*diaheliotropism*). The response of the isobilateral and of the radial leaf to the action of gravity is one of negative geotropism, so that they grow erect; and to light, one of positive heliotropism, as they tend to direct their apices towards the source of light.

Fig. 470 (after Darwin).—Shoots of *Desmodium gyrans*, with trifoliolate leaves: *A* leaves in diurnal position; *B* in nocturnal position.

Changes in the external conditions act as stimuli, which, in many cases, induce a movement of the foliage-leaves involving change of position: most frequently these movements are performed by growing leaves, but also sometimes by adult leaves with a permanent motile mechanism. They have been observed in the growing leaves (and cotyledons) of many plants (*e.g.* Chenopodium, Impatiens, Polygonum, Linum, etc.), and in the adult leaves of many Oxalidaceæ and Leguminosæ. The common feature of these movements is that they serve to vary the area of surface presented to the sky by the leaf. They are commonly known as "sleep-movements," or *nyctitropic* movements, because they are usually associated with the alternation of day and night. With a falling temperature and a diminishing intensity of light the leaves assume the "night-position," presenting a diminished surface, generally only the edge, to the zenith, the leaflets of compound leaves at the same time approaching each other, with the result that they are protected from injury by cold in consequence of excessive radiation of heat: with a rising temperature and an increasing intensity of light, the leaves assume the "day-position," presenting their upper surfaces to the zenith. But the day-position is frequently liable to modification, with a view to the reduction of transpiration and to the protection of the chlorophyll from the action of too intense light, by movements which diminish the leaf-area exposed to the direct rays of the sun;—and so, in some cases, the edge, and not the upper surface, is presented to the sun: these movements are designated "diurnal sleep" or *paraheliotropism.*

Fig. 471.—Leaf of Oxalis by day (*T*) and by night (*N*). In the latter, each leaflet is folded inwards at right angles along its midrib, and is also bent downwards.

Some foliage-leaves, but only such as have a special motile mechanism, respond by movement to the stimulus of a touch. This is the case in the "sensitive plants," such as *Mimosa pudica* and other species, *Biophytum* (*Oxalis*) *sensitivum*, *Æschynomene indica*, *Neptunia oleracea*: the leaflets of the pinnate leaves of these plants close together when touched, or when the plant is shaken, and they are thus protected to some extent from injury by hail, rain, or even wind. Other instances of movement in response to touch are afforded by the "carnivorous" genera, Dionæa and Aldrovanda, in which, when an insect alights on the upper surface of the expanded leaf and touches the sensitive hairs, the two lateral halves of the blade suddenly close together, like a hinge, with the midrib as the axis.

Sensitiveness to long-continued contact is manifested by the petioles of various plants (*e.g.* Tropæolum, Clematis); sometimes by the whole phyllopodium (Lygodium); in many cases leaves possessing this sensitiveness are modified into leaf-tendrils (see p. 58; as in Cucurbitaceæ, etc.); leaves of this kind serve as organs of attachment for climbing.

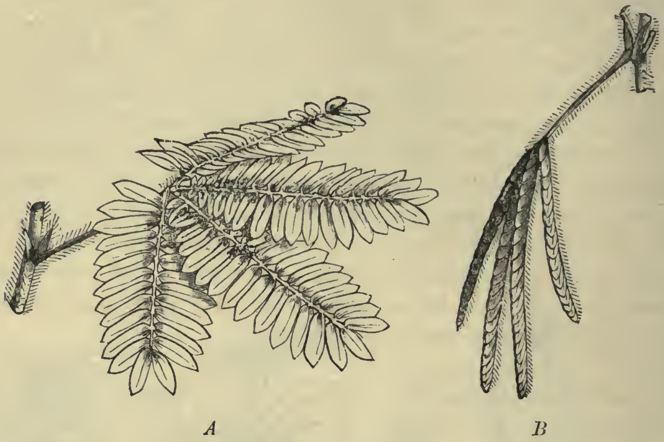

FIG. 472 (after Duchartre).—Leaves of *Mimosa pudica*: *A* normal diurnal position; *B* position assumed on stimulation.

FIG. 473 (after Darwin).—Petiole of *Solanum jasminoides* clasping a stick.

Foliage-leaves are sometimes modified into *pitchers* or *ascidia* (p. 57): these serve the purpose in some cases (*e.g.* Nepenthes) of capturing insects and of digesting and absorbing them: in other cases (*e.g.* Dischidia) they collect water and organic detritus; in Dischidia adventitious roots are developed, which lie in the pitchers and absorb water, together with dissolved substances, therefrom.

Leaf-spines appear to be exclusively protective against the attacks of herbivorous animals.

(2). *Cataphyllary or Scaly Leaves* (p. 58) serve to protect growing-points and young leaves of buds, and in this they are assisted by the secreting-hairs (colleters, p. 144) which they frequently bear: they sometimes serve as depositories of reserve plastic materials (*e.g.* scales of Onion-bulb).

(3). *Floral Leaves.*

a. Hypsophyllary Leaves. The leaves included under this head are the bracts (and bracteoles) and the perianth-leaves (p. 59).

When green, the *bracts* perform the ordinary functions of foliage-leaves: but when they are collected around a flower (epicalyx) or an inflorescence (*e.g.* involucre of Compositæ, Euphorbia, etc.) they serve to protect the floral organs during their development. When highly-coloured (*e.g.* in Araceæ, Euphorbiaceæ, Nyctaginaceæ), they serve to attract insects to visit the otherwise inconspicuous flowers.

The *sepals*, like the bracts, are commonly green, and then they perform the ordinary functions of foliage-leaves, and also serve to protect the other floral organs: when petaloid (*e.g.* many Ranunculaceæ and Liliales), they attract insects for the purpose of cross-pollination.

The *petals* are brightly-coloured in most flowers, and it is their special function to attract insects. Not uncommonly they are specially modified as nectaries (*e.g.* Helleborus), and thus further contribute to ensure the visits of insects.

The perianth-leaves (and sometimes also the bracts), are often capable of performing movements leading to the opening and closing of the flower or inflorescence: thus the flowers of the Crocus, Tulip, and Poppy, and the inflorescence of the Daisy, open under the influence of rising temperature and increasing intensity of light, closing under the contrary conditions: the closing is a protection of the essential floral organs against cold and wet; it is essentially similar to the nyctitropic movements of foliage-leaves (see p. 689).

b. Sporophyllary Leaves. As already stated (p. 77) the sporophylls are the essential organs of the flower, when they are aggregated on a special shoot, and have, in any case, the function of asexually producing the spores. They are more or less generally modified in form and structure in connexion with this function; and in the many different forms of flowers these leaves present remarkable special adaptations which mainly refer to the process of pollination (see p. 452), to the distribution of the seed, etc. It is impossible to enter upon a further consideration of the biology of the flower, but the phenomena of movement presented by the essential floral organs deserve special mention.

A remarkable case of spontaneous movement is that of the gynostemium of *Stylidium* (*Candollea*) *adnatum*, the object of which is the scattering of the pollen, and it accordingly begins when the anthers are about to dehisce: the gynostemium bends over till it touches a gland on the anterior petal, and to this it adheres until it straightens and frees itself from the sticky gland with a jerk which scatters the pollen; the movement is then repeated.

Induced movements are more common. Thus the two lobes of the stigma (*e.g.* Mimulus, Bignonia, Martynia), close together on being touched: the movement doubtless ensures the adhesion of the pollen brought by an insect. The stamens are irritable in many plants. For instance, in Berberis, when an insect touches the irritable base of one of the nearly horizontal stamens, the stamen rises up on its point of attachment as on a hinge, and strikes the insect with the anther, thus dusting it with pollen. Again, the syngenesious stamens of Centaurea (p. 664) shorten on stimulation by touch: the flower is protandrous; consequently, as the filaments contract, the pollen shed by the coherent anthers is pushed out of the open end of the anther-tube by the style within, and is removed by the insect.

CHAPTER II.

SPECIAL PHYSIOLOGY OF THE NUTRITIVE FUNCTIONS.

§ 6. **Absorption.** The food of plants is absorbed, generally speaking, either from the soil or from the air.

Plants which do not possess chlorophyll (*e.g.* Fungi) usually obtain the whole of their food from the soil; whereas plants which do possess chlorophyll absorb from the air one of the most important constituents of their food, namely carbon dioxide.

In exceptional cases it is obtained from other sources; for instance, parasitic plants absorb their food from the hosts upon which they live, and the "insectivorous" plants absorb a portion, at least, of their food, from the insects which are caught by their specially adapted leaves. Submerged aquatic plants absorb their food entirely or mainly from the water in which they live.

As already mentioned (p. 668), the food of plants is always absorbed in the fluid form; either as a liquid or as a gas. The liquid food, consisting of a watery solution of various substances, is absorbed from the soil most commonly by the roots, or, in the absence of roots, by other members (shoots, leaves) which have become specially adapted for the performance of this function; the gaseous food (CO_2) is absorbed from the air by the green parts (shoot) of plants, and, in the more highly differentiated forms, more especially by the leaves.

Absorption of Liquids. When an organ which is adapted for the absorption of liquids is performing its function, two processes are in operation, namely, the absorption of the water, and the absorption of the substances which the water holds in solution: it is important to clearly distinguish between these two processes, for though they are necessarily carried on simultaneously, yet the water and the dissolved substances are not absorbed in any constant proportion. The two processes, in fact, depend upon somewhat different conditions. The cells of the absorbent organ take up the water in consequence of the presence in solution in the cell-sap of osmotically active substances, such as organic acids and acid salts, which attract water into the cells. The substances in solution in the water are absorbed in virtue, first, of their diffusibility, that is their power of passing through membranes, and secondly, of the fact that the cell-sap in the interior of the absorbing cells contains less of the substances in question than does the water outside. Hence any indiffusible substance which may be dissolved in the water will not be absorbed by the cells, neither will any substance of which there is already an equivalent quantity in solution in the sap of the cells, although the absorption of water may be actively taking place. These facts find their general expression in the following statement which is known as the *Law of Absorption*: for the watery solution of any substance capable of being absorbed, there is a certain degree of concentration at which the proportion of the amount of the substance absorbed to that of the water absorbed is the same as that of the solution; if the solution be more concentrated, the proportion of water absorbed will be greater, and that of the substance less; if the solution be more dilute, the proportion of the substance absorbed will be greater, and that of the water less.

When, as is usually the case, the liquid with which the absorbent cells come into relation, is a solution of a number of different substances, these different substances are not all absorbed in the same proportion. Supposing the absorbing organ to be equally poor in all these substances. Then, in the first instance, the substances would be absorbed in proportion to their diffusibility, the most diffusible being absorbed the most rapidly. Subsequently, however, the relative amount of substances absorbed would be determined by the extent to which, after absorption, they severally were chemically altered in the metabolism of the plant. For when a substance is chemically altered in the plant, it ceases to exist, as such, in the sap of the cells; hence, when a substance is constantly being decomposed in the plant, it can be also contantly absorbed. When, on the other hand, an absorbed substance does not undergo chemical change in the plant, it accumulates in the sap of the cells, and consequently the absorption of it from without eventually ceases.

This point can be determined with regard, at least, to the mineral substances which a plant absorbs, by an analysis of the *ash* which is left behind on incinerating the plant, that is, on burning away the combustible organic matter. The ash will be found to include all the mineral elements present in the soil or water from which absorption is taking place, in so far as those elements are present in the form of compounds which are soluble and diffusible. The general constitution of the ash depends upon the chemical nature of the soil, and upon the physical properties of the substances which comprise it, as is proved by the fact that the constitution of the ash of any given plant varies with the soil in which it grows. But the relative proportion of the various chemical elements in the ash depends upon the capacity of the plant to chemically alter the various compounds which it absorbs, as is proved by the fact that the constitution of the ash varies widely in plants of different kinds grown in the same soil; it is the expression of the specific metabolic properties of the plant, or, in other words, of the *specific absorbent capacity* of the plant. And not only has each plant a specific absorbent capacity, but this varies at different periods in its development, in harmony with the variation which takes place in its metabolic processes.

A good illustration of the different specific absorbent capacities of plants is afforded by a comparison of the amount of silica in the ash of different plants. Thus, an analysis of meadow-hay and of pea-straw, grown under the same conditions, showed that the former contained 27 per cent. of silica, and the latter scarcely 7 per cent. This is due to the fact that the Grasses deposit considerable quantities of silica in their cell-walls, whereas Peas are unable to do this to anything like the same extent.

It not infrequently happens that chemical elements are found to be present in the ash, which are known to be present in the soil in the form of compounds which are insoluble in water. These compounds are brought into solution by various means. For instance, the soil usually contains carbon dioxide, which is evolved from the decomposing animal or vegetable matter which is commonly present, and from the absorbent organs themselves; and it is well known that various substances, such as calcium carbonate and certain silicates, which are insoluble in pure water, are soluble in water charged with carbon dioxide. Again, the sap which fills the vacuoles and saturates the walls of root-hairs, has an acid reaction, due to the presence of organic acid, and this acid sap will dissolve many substances which are insoluble in pure water. The solvent effect of this acid sap is well demonstrated by means of the familiar experiment with a slab of marble. If a highly-polished slab of marble be fixed in the bottom of a flower-pot, and a plant be grown in the soil above it, the roots will come into contact with the slab and will apply themselves to its surface. On subsequently examining the slab of marble, it will be found to have become corroded where the roots had been in contact with it. The corrosion is due to the solution, by the acid sap of the roots, of particles of the marble.

The activity of the absorption of water is dependent upon the temperature. For example, the absorption of water by roots begins at a minimum temperature; it increases in activity as the temperature rises to optimum; any further rise of temperature is attended by a diminished activity of absorption.

Absorption of Gases. The absorption of gases depends, like the absorption of water and substances in solution, upon diffusion. Supposing an absorbent cell, the sap of which holds, to begin with, no gases in solution, to be brought into relation with a mixture of gases, these gases will be dissolved at the surface in proportion to their solubility and to the amount of each gas present in the mixture, that is, the amount absorbed of each gas depends, in the first instance, upon its solubility and its partial pressure. The relative amount of each gas absorbed over a period of time will further depend upon the extent to which it undergoes chemical alteration after absorption. For instance, plants absorb from the air nitrogen, oxygen, and carbon dioxide under certain circumstances. On account of the greater proportion of nitrogen in the air, this gas will be, in the first instance, absorbed to a larger extent than either of the others. But inasmuch as the nitrogen does not enter into the metabolic processes of the plant, whereas oxygen and, under certain circumstances, carbon dioxide, do so, the nitrogen simply accumulates in the cell-sap, and the absorption of it will soon cease, whereas the absorption of the oxygen and of the carbon dioxide will continue.

Land-plants absorb gases, in the manner described above, at all points of their surface; by their shoots from the air, by their roots from the gaseous mixture in the interstices of the soil; the stomata of the sub-aerial parts are of great importance in connexion with this process. Submerged water-plants absorb, in solution, the gases dissolved in the water.

The absorbed gases remain in solution in the cell-sap, so that living cells do not contain bubbles of gases. Moreover, gases travel in the plant mainly by diffusion from cell to cell, though their distribution may also be effected by means of the intercellular spaces.

The particular gas which may be regarded as a food-material is carbon dioxide. Although the amount of this gas to be found in the air, or in solution in water, at any given moment, is usually small, yet inasmuch as the supply is maintained, enough of it can be obtained for the needs of the plant. The conditions of its absorption are the following: First, it is only absorbed by those cells which contain chlorophyll; Secondly, it is only absorbed by these cells when exposed to light of a certain intensity, the most active rays being those of low refrangibility.

§ 7. **Transpiration.** Every part of a plant which is exposed to the air, except such as are covered by a thick layer of cork, is continually exhaling watery vapour. This may be demonstrated by placing a leafy branch under a bell-glass, when it will shortly be observed that the internal surface becomes covered with drops of water, the watery vapour exhaled by the branch having condensed upon the cold glass. Again, the drooping of cut flowers or herbaceous branches is due to the loss of water by transpiration.

It must be clearly understood that transpiration is not simply evaporation. If it were so, then clearly equal amounts of water would be evaporated in a given time by equal areas of water-surface, and of living plant-surface. But this is not the case. All observations show that the amount of water transpired from a given area of living plant-surface in a given time, is only a small fraction of that evaporated in the same time from an equal surface of water. On the other hand, the evaporation from dead plant-surface is as active, or even more so, than from a free surface of water. Transpiration, whilst ultimately depending upon the purely physical process of evaporation, is essentially evaporation modified by the living substance, protoplasm, from and through which it takes place, and is therefore a vital function.

The activity of transpiration is intimately connected with the external conditions. It is dependent upon the hygrometric state of the atmosphere, upon the temperature of the air, and especially upon exposure to light. Naturally, the drier the atmosphere the more active the transpiration; and, similarly, a rise of temperature promotes transpiration. The effect of exposure to light is very striking. On removing a plant from darkness to even feeble light, its transpiration is markedly increased; but when it is removed into bright sunlight it is increased severalfold. This effect of light is especially marked in the case of plants, or parts of plants, which contain chlorophyll. It is clear that light so acts upon the protoplasm of the transpiring tissue as to facilitate the evaporation of the water contained in the cells.

The activity of the transpiration from the surface of a plant is inversely proportional to the development of the tegumentary tissue. Thus, transpiration is rapid in the case of stems and leaves in which cuticularisation or suberisation of the superficial cell-walls has taken place to but a small extent or not at all, whereas the transpiration of organs which, like the trunks of many trees, are covered externally by layers of cork, or which, like the stems and leaves of succulent plants, such as Cacti, Aloes, Crassulaceæ, etc., have a thick cuticle, is comparatively slight.

However, inasmuch as most aerial leaves and stems have a more or less well-developed and cuticularised tegumentary tissue, the transpiration from the external surface is insignificant. In such cases the transpiration takes place mainly through the thin uncuticularised walls of the cells of the ground-tissue into the intercellular spaces, and the watery vapour escapes from the intercellular spaces into the external air by means of the stomata and the lenticels. The stomata, especially, are organs for the regulation of transpiration. As already mentioned (p. 156), the stomata open and close, their opening and closing being dependent upon variations in the turgidity of the guard-cells. When the guard-cells are highly turgid, they curve so as to separate from each other in the middle line, thus opening the stoma; when they are flaccid, their free surfaces are brought into contact, and the stoma is closed. It was held for a long time that the opening and closing of the stomata depended mainly on whether or not the plant was exposed to light; that the stomata opened in bright light and closed in darkness; and that the more active transpiration in light than in darkness was attributable to the condition of the stomata. But it is now known that the opening or closing of the stomata is not thus directly dependent on light, but is a function of transpiration as affected by the hygrometric condition of the air, and by the supply of water in the plant: so that when the transpiration is normal, as determined by a certain relation existing between the hygrometric condition of the air and the supply of water to the transpiring leaf, the stomata are open; but when transpiration becomes excessive, by the air becoming drier, or by a diminution in the supply of water to the leaf, the stomata close, even before any trace of flagging is shown by the leaf. Thus the stomata act as regulators of transpiration, and their opening or closing depends partly on external and partly on internal conditions.

The water lost by transpiration is supplied to the transpiring organs from the roots. If the loss by transpiration is compensated by the absorbent activity of the roots, the transpiring organs remain fresh and turgid. But if, as is frequently the case on a hot summer day, the loss of water by transpiration is greater than the supply from the roots, the transpiring organs, more especially the leaves, become flaccid and droop, and they are only restored to the turgid condition in the evening when the temperature of the air falls and the intensity of the light diminishes; in a word, when the external conditions become such as to lead to a diminution of the transpiration.

There is, however, besides the flaccidity of the herbaceous members of the plant, another means of observing the effect of transpiration upon the amount of water contained in the tissues. If the stem, or a branch, of an actively transpiring plant be cut through under mercury or some other liquid, it will be observed that the liquid will at once make its way for a considerable distance into the woody tissue of the cut stem or branch. This is due to the fact that, in consequence of the withdrawal of water from them, the gases in the vessels are at a lower pressure than that of the atmosphere. This is termed the *negative pressure* in the vascular tissue.

These various points can be readily observed in low-growing plants, such as the cabbage. On a hot summer day the leaves become flaccid, and the existence of a negative pressure in the vessels of the stem can be ascertained. In the evening, when the activity of transpiration is diminished, but active absorption of water from the warm soil by the roots continues, the leaves become turgid, and water gradually accumulates in the vascular tissue. During the night this accumulation of water in the vascular tissue goes on until it becomes quite full, so that there comes to be not only no negative pressure, but a positive pressure. This positive pressure, were there no means of relieving it, might become injurious to the tissues; but it is relieved by the filtering of drops out of the closed terminations of the vascular bundles in the leaves, these drops making their way to the surface through openings over the ends of the bundles, which are either the ordinary stomata, or the specially-modified water-stomata. A row of such drops on the margin of the leaves may be observed in many plants in the early morning. It appears, then, that during the day the loss of water by transpiration is greater than the supply by absorption, whereas during the night the contrary is the case.

With regard to the physiological significance of transpiration, it is important in that it causes a rapid current of liquid, the *transpiration-current*, to flow through the plant from the roots to the transpiring organs, more especially the leaves. This ensures the distribution, not only of the absorbed water, but also of the substances absorbed in solution from the soil. It will be noticed that the conditions which promote transpiration, namely, light and warmth, are just those which are most favourable to the performance of their anabolic processes by the organs which contain chlorophyll. Thus, when the leaves are actively producing organic substance, they are actively transpiring, and they are therefore constantly receiving supplies of the substances absorbed from the soil, substances some at least of which are essential to the chemical processes in operation. Transpiration has, then, an important bearing upon nutrition. There seems to be, in fact, an optimum activity of transpiration, that is to say, a certain activity of transpiration which promotes to the utmost the formation of organic substance; so that if the average activity of transpiration falls short of, or exceeds, this optimum, the nutrition of the plant suffers, as shown by a diminished formation of organic substance.

§ 8. **Distribution of Water and other Substances.** It is clear that, when the plant-body is so far differentiated that only certain parts of it are in a position to absorb water and substances in solution from without, there must be a distribution of the absorbed substances from the absorbent surfaces to the other parts. Further, when the plant-body is differentiated into parts which do, and others which do not, contain chlorophyll, there must be a distribution of the produced organic substance from the former to the latter.

In plants of relatively low organisation, the distribution takes place entirely by diffusion; by simple diffusion when the plant is a cœnocyte; by diffusion through the cell-walls, that is by osmosis, when the plant is multicellular: and even in the highest plants diffusion plays an important part.

With regard, first, to the distribution of water and substances absorbed in solution from without, in the more highly organised plants. In these plants, as already stated, the conducting tissue is the wood or xylem of the vascular bundles, extending from the roots, the absorbent organs, to the leaves, the transpiring organs.

With regard to the mechanism by which the water absorbed by the roots is conveyed to the leaves, it must, in the first place, be clearly understood that, as already mentioned (p. 678), the xylem does not communicate directly with the atmosphere, but is a completely closed tissue-system. The mode in which water and substances in solution are introduced into this closed tissue-system in the root is as follows:—The root-hairs absorb water from the soil; the absorbed water passes by osmosis from the root-hairs into the adjacent cortical parenchymatous cells of the root; these cells become highly turgid, and when a certain degree of turgidity is attained, the water escapes by filtration under pressure from the innermost parenchymatous cells into the xylem-vessels upon which they abut. The water is thus forced into the xylem under considerable pressure, which is termed the *root-pressure.* In the leaves, water is withdrawn from the xylem by the adjacent cells which absorb it osmotically, and from these in turn by those which are actually transpiring.

The Root-Pressure. The existence of the root-pressure can be easily ascertained. It is manifested spontaneously by that exudation of drops on the margin of the leaves of low-growing plants during the night, to which allusion has already been made (p. 699). An artificial manifestation of it is induced in stems which are cut across at a time when, owing to active absorption and feeble transpiration, the plants are rich in water; drops exude from the xylem-vessels at the cut surface of that part of a stem which is still in connexion with the root. A familiar case of this is the "bleeding" of certain shrubs and trees when pruned in the spring. It is possible, in this way, to estimate both the activity and the force of the root-pressure. By collecting the water which exudes from the cut surface of the stem, the amount of water absorbed by the root in a given time is determined; and by attaching a mercurial manometer to the cut surface of the stem the force of the root-pressure can be measured. For instance, 3,025 cubic millimetres of liquid were collected from a Stinging Nettle in 99 hours; and the root-pressure required a column of mercury 354 millimetres in height to counterbalance it: in other words, the root-pressure of the Nettle was nearly half an atmosphere, and was capable of supporting a column of water about 15 feet high.

The essential point in the mechanism of the root-pressure is the forcing of liquid by filtration under pressure from the parenchymatous cells into the xylem. The process is probably to be explained somewhat in this way. When a certain degree of turgidity is attained in the parenchymatous cells abutting on the xylem, their motile protoplasm undergoes a molecular change, in consequence of which it becomes permeable and ceases to offer resistance to the escape of the cell-sap; consequently, under the elastic contraction of the distended cell-walls, a portion of the cell-sap is forced out of the cell. This molecular change in the state of aggregation of the protoplasm of the parenchymatous cells probably takes place at more or less regular intervals, so that there is a sort of rhythmic pumping of liquid into the xylem of the root. From this point of view, the root-pressure of a plant is simply the expression of the force of the elastic contraction of the cell-walls of the parenchymatous cells abutting on the xylem-bundles in the root.

With regard to the external conditions which affect the root-pressure, the most important is the temperature of the soil; a rise of temperature up to the optimum increases the root-pressure, but any further rise causes it to diminish, and if the soil be heated so as to kill the roots, the root-pressure altogether disappears. In any case the force of the root-pressure is not uniform, but varies; and the more considerable variations occur in such a way as to constitute a well-marked daily period. The exact periodicity depends partly on the age of the plant, and partly on the conditions under which it has been living: it may be generally described as follows:—The force of the root-pressure is least during the early morning hours; it then gradually increases, reaching its maximum early in the afternoon, and then it diminishes during the evening and night until the minimum is attained early the following morning. Thus there is a period of about twelve hours between the occurrence of the minima and the maxima, and there can be no doubt that this periodicity has been induced by the periodic changes in the external conditions accompanying the alternation of day and night.

The liquid forced into the tracheal tissue is by no means pure water; it holds various substances in solution, such as mineral salts absorbed from the soil; in the spring it is relatively rich in organic substances, such as proteids, sugar, acids, colouring-matters, etc., derived from the reserves stored in the parenchymatous cells of the root, which are being conveyed to the opening buds.

The Transpiration-Current. The mechanism by which, after the liquid has been forced into the xylem of the root, a sufficient current is maintained through the stem of a lofty tree to supply the actively transpiring leaves, is still one of the incompletely solved problems of physiology.

It might be assumed that the transpiration-current is maintained simply by the root-pressure. There is no doubt that, in low-growing plants (see p. 701), the root-pressure is sufficient to force liquid to all parts of the plant; and this is probably true also of lofty trees. The objection is that no root-pressure can be detected at any time in a great many plants, and that it can never be detected in any plant at the time when transpiration is active, when, on the contrary, there is negative pressure (p. 699) in the vessels. Moreover, a transpiration-current is maintained for a time by entire plants whose roots have been killed by heat, as also by cut-off shoots.

It has been suggested that the current is maintained by a repetition of the root-pressure-action at various levels in the stem, water being absorbed and then returned under pressure into the vessels by the adjacent parenchymatous cells. This view, based principally on anatomical facts, is supported by but little direct evidence, although it has been ascertained in certain cases that the parenchymatous cells of the stem are capable of forcing liquid into the xylem: for instance, when a piece of a grass-haulm is placed with its lower end in wet sand, drops of water may be observed to exude from the upper cut surface after a time. But in view of the fact that the transpiration-current can be maintained through a considerable length of stem killed by heat, as also of the fact that fatally poisonous solutions may be thus conveyed upwards through the wood for a length of time which ensures the death of all the adjacent parenchymatous cells, it is difficult to see how this theory can be maintained.

It has also been suggested that the current is due to purely physical causes, such as capillarity and the difference between the pressure of the external atmosphere and the lower pressure of the gases in the xylem of the plant, or the differences of pressure of the gases in the lower and upper parts of the plant. With regard to capillarity, it need only be pointed out that in many cases (*e.g.* Coniferæ) the conducting-tissue of the xylem does not consist of continuous capillary tubes, but of closed tracheids; here it is impossible for a column of water to be raised by capillarity, and yet the current is maintained; and even in plants with continuous xylem-vessels, the force of capillarity would be altogether inadequate for the maintenance of the current. With regard to the "gas-pressure-theory," it will suffice to point out that, even if it were well-founded, it could only account for the raising of water in the plant to a height of thirty-two feet at the utmost; but it is not well-founded, for inasmuch as the xylem-system is air-tight, being shut off from all communication with the external air (see p. 678), the movement of fluids within it is in no degree affected by the atmospheric pressure, and the internal differences of gas-pressure are altogether inadequate. However, though neither capillarity nor differences of pressure can be regarded as the active cause of the current, the maintenance of the current is affected both by the capillarity of the vascular tissue through which it travels, and by the varying pressure of the gases which that tissue may contain.

Two facts have been made clear by the foregoing considerations: first, that the water contained in the wood is readily mobile, a fact which has been proved beyond question by special experiments: second, that the only force remaining to which the movement of the transpiration-current in the stem can be attributed, is that of the osmotic absorption of water from the tracheal tissue by the adjacent cells of the leaves when transpiration is going on. In accordance with these facts it has been suggested that the water travels molecularly through the substance of the lignified cell-walls, the water taken up from the wood by the transpiring leaves being at once replaced by fresh molecules coming up from below. The merit of this view, known as the "imbibition-theory," is that it overcomes the difficulty of accounting for the raising of water through the cavities of the tracheal tissue; for the molecules of the water thus conceived of as being held in the substance of the cell-walls will travel, like the molecules of a gas, in the direction of least resistance, that is, towards the transpiring organs. Moreover it is true that the transpiration-current will only travel through wood the walls of which are saturated with water. But it is objected to this theory that it does not accord with the fact that any diminution or interruption of the lumina of the vessels, by compression for instance, or by section, diminishes or arrests the transpiration-current; clearly this ought not to be the case if the current travels exclusively in the walls. Moreover it has been ascertained that the actually conducting-tissue of the wood always contains water in its cavities even when transpiration is most active, though bubbles of gas are also present, at any rate in the wider vessels or tracheids.

The conclusions to be drawn as to the mechanism of the transpiration-current in lofty trees, may be stated as follows. In the spring the wood is full of water forced into it by root-pressure. When the leaves unfold, and begin to transpire, water is gradually withdrawn from the conducting tracheal tissue, and the tissue is, at any rate for the most part, occupied by a system of short columns of water with intervening gas-bubbles, the columns of water being in communication by delicate films along the cell-walls. If the whole of the tracheal tissue be in this state, it is suggested that as water is withdrawn from the upper part of the wood by the transpiration of the leaves, a current is set up, the water travelling along the cell-walls, between them and the gas-bubbles. But it may be that a continuous system of tracheids completely filled with water is maintained, and that it is through this that the current travels. The conducting-tissue is supplied with water, in the first instance, from that which fills the non-conducting tissue of the wood (and the old wood or duramen, if present), and ultimately by the root. It may be thought that the suction due to transpiration would be incapable of maintaining the current; but this difficulty is met by the consideration that the water is held in position by the capillarity and the cellular structure of the tracheidal tissue, and that the system of columns of water and gas-bubbles does not move as a whole, since the latter cannot pass the pit-membranes of tracheids. Moreover the force of transpiratory suction is considerable, though it has not been accurately measured.

The Distribution of Organic Plastic Substances. These substances may be generally stated to consist of organic substances of two kinds, nitrogenous and non-nitrogenous, and these are distributed through different channels.

1. The *nitrogenous* substances travel, in plants or in parts of plants which are not supplied with vascular tissue, in the form of amides (see p. 707) by osmosis from cell to cell. But in vascular plants it is known that they also travel in the sieve-tissue from one member of the plant to another, in the form of indiffusible proteids. There is no evidence that the very slow movement of the contents of the sieve-tubes is effected by any special mechanism; it appears to be simply induced by the demand for these substances at any points, and it is doubtless promoted by the swaying of the stem and branches.

2. The *non-nitrogenous* substances travel through the plant in the form of glucose and maltose (see p. 708), in solution; they travel by diffusion from cell to cell, and more especially in the elongated parenchymatous cells, forming the *conducting-sheath*, which, in the leaf, consists of mesophyll-cells closely investing the vascular bundles, and, in the stem, belongs to the inner cortex. This layer is not the endodermis, but lies externally to it; the endodermis frequently contains starch-grains, and is sometimes termed the *starch-sheath*, but it is rather a depository than a conducting-tissue.

The direction in which organic substances travel in the plant seems to be determined simply by the demand for them. Just as the water and the substances in solution absorbed by the roots travel to the transpiring and assimilating organs, so the organic substances produced in the assimilating organs travel in the plant to those parts in which organic substance is either being used in growth, or is being stored up as reserve material. In a Potato-plant, for example, part of the organic substance formed in the leaves travels to the growing-points of the roots and of the shoots, where it is required for the development of new leaves, flowers, branches, etc., whilst the residue travels to the underground shoots which are developing into tubers and are storing up quantities of starch. Similarly, these organic substances travel apparently by the same channels and in the form of the same chemical compounds, from organs which serve as depositories of reserve material, when these stores are drawn upon to supply the growth of developing parts. For instance, when a Potato-tuber begins to sprout, the starch, which is the principal reserve material, is drawn upon, being gradually converted into sugar, in which form it travels to the growing-points of the young shoots and supplies a large proportion of the plastic material necessary for their growth.

§ 9. **Metabolism.** This subject will be subdivided into: 1, Chemical Composition; 2, Food of Plants; 3, Anabolism; 4, Catabolism; 5, Products of Metabolism; 6, Supply and Expenditure of Energy.

1. *Chemical Composition.* As a preliminary, a general account of the chemical composition of plants will be given.

All parts of living plants contain a considerable quantity of water: this forms not merely the principal constituent of the cell-sap, but also saturates the cell-walls, the protoplasm, in short, all organised structures; it is, in fact, one of the peculiarities of organised structures that minute particles of water are interposed between the particles of solid matter of which they consist. By heating to 100° or 110° C., all the water contained in any part of a plant is expelled, and in consequence it will naturally lose weight. The amount of this loss, that is, the quantity of contained water, is very different in various plants; ripe seeds dried in the air contain from 12 to 15 per cent. of water, herbaceous plants 60 to 80 per cent., and many water-plants and Fungi as much as 95 per cent. of their whole weight.

The residue, which gives off no more water at a heat of 100° C., the dry solid, consists of a great variety of chemical compounds; these are partly *organic*, that is to say, combinations of carbon with other elements, and partly *inorganic.* These organic substances which occur in the living plant (with the exception of salts of oxalic acid) all contain hydrogen. Some of them, such as many oils, consist of these two elements only (carbon and hydrogen), but by far the greater number, including cellulose, starch, and sugar, as well as the vegetable acids and certain oils, contain oxygen also. The proteid substances consist of carbon, hydrogen, oxygen, nitrogen, sulphur, and sometimes phosphorus; in other bodies which contain nitrogen, as asparagin and many alkaloids, there is no sulphur or phosphorus; from certain other alkaloids, for instance nicotin, oxygen is also absent.

The commoner organic substances of which the plant-body consists may, in the first instance, be divided into those which do and those which do not contain nitrogen in their molecule.

The most important *nitrogenous* substances may be classified as follows:—

1. *Proteids:* these are substances with a large molecule of complex constitution, to which no chemical formula has yet been assigned; they may be soluble or insoluble in water, and when soluble are mostly indiffusible; they are generally of a viscid nature (like white of egg) and are rarely crystallisable. Of these there are several varieties:—

a. Insoluble Proteids: do not dissolve even in dilute acids or alkalies: *e.g.* coagulated proteid.

b. Albuminates: insoluble in water or solutions of neutral salts, but soluble in dilute acids or alkalies, sometimes soluble in dilute alcohol: *e.g.* gluten of wheat.

c. Globulins: insoluble in water, but soluble in solutions of neutral salts (such as NaCl) and coagulated on boiling, sometimes crystallisable: these enter largely into the composition of aleuron (see p. 112); the crystalloids in the potato and in some aleuron-grains (*e.g.* Ricinus, Bertholletia) consist of a kind of globulin (vitellin).

d. Albumins: soluble in water, coagulated on boiling: rare.

e. Albumoses: soluble in water, not coagulated on boiling, but precipitated by a small quantity of nitric or acetic acid, and soluble in excess: a common constituent of aleuron.

f. Peptones: soluble in water, not precipitated by boiling or by acids; present in germinating seeds.

2. *Amides* (or Amido-acids): these substances are soluble in water, not coagulated on boiling, diffusible, and crystallisable. Those commonly occurring in plants are Asparagin ($C_4H_8N_2O_3$), Leucin ($C_{12}H_{23}N_2O_4$), Tyrosin ($C_9H_{11}NO_3$).

3. *Alkaloids:* these substances are, chemically, organic bases, occurring in plants in combination with organic acids; they are insoluble or but slightly soluble in water, soluble in alcohol; most of them are solid at ordinary temperatures, and are crystalline, whilst others are liquid (Coniin, Nicotin); they are generally poisonous.

The more familiar alkaloids are Coniin ($C_8H_{15}N$) from Conium; Nicotin ($C_{10}H_{14}N_2$) from Tobacco; Morphin ($C_{17}H_{19}NO_3$), and other opium-alkaloids from the Poppy; Strychnin ($C_{21}H_{22}N_2O_2$) from *Strychnos Nux vomica*; Quinin ($C_{20}H_{24}N_2O_2$) from the Cinchona; Thein ($C_8H_{10}N_4O_2$) from Tea; Theobromin ($C_7H_8N_4O_2$) from *Theobroma Cacao.*

Some *colouring-matters* are also nitrogenous (*e.g.* chlorophyll, and indigo C_8H_5NO), as also some glucosides (see below).

The principal *non-nitrogenous* substances are :—

1. *Carbohydrates :* substances consisting of C, H, and O, the H and O being present in the same proportions as in water (H_2O) ; of these there are the following classes :

a. *Amyloses :* general formula n ($C_6H_{10}O_5$) ; of these *cellulose* and *starch* are the most common, the former entering largely into the composition of cell-walls, the latter occurring as a reserve material in the form of starch-grains ; they are neither of them soluble in water under ordinary circumstances : *dextrin* or *amylin*, a product of the action of diastase on starch, is soluble in water but not crystallisable : *inulin* occurs in many Compositæ and allied orders (Campanulaceæ, Lobeliaceæ) in solution in the cell-sap ; it is slightly soluble in cold water and is crystallisable. The gums and mucilages also belong to this group.

b. *Sucroses :* $C_{12}H_{22}O_{11}$: soluble in water and crystallisable : cane-sugar occurs in many plants (esp. Sugar-cane and Beetroot) ; maltose is the chief product of the action of diastase on starch.

c. *Glucoses :* $C_6H_{12}O_6$: soluble in water and crystallisable : they occur in fruits (grape-sugar).

The sucroses and glucoses are commonly known as sugars.

A substance termed *Mannite* ($C_6H_{14}O_6$) occurs in the cell-sap of *Fraxinus Ornus* and some other plants : though not a carbohydrate, it is closely allied to this group ; crystallisable, but not readily soluble in water. The glucoses are derivatives (aldehydes) of mannite (an alcohol).

2. *Organic Acids :* these occur in the plant either free or, more commonly, as neutral or acid salts in combination with organic or mineral bases ; some are constituents of the fats and fixed oils (*e.g.* palmitic and oleic acids ; see below) : the more common are oxalic acid ($H_2C_2O_4$), malic acid ($H_2C_4H_4O_5$), tartaric acid ($H_2C_4H_4O_6$), citric acid ($H_3C_6H_5O_7$).

3. *Glucosides :* substances of complex constitution which owe their name to the fact that they give rise, on decomposition, to glucose among other products : such are *amygdalin*, $C_{20}H_{27}NO_{11}$ (seeds, etc., of many Rosaceæ) ; *coniferin*, $C_{16}H_{22}O_8$ (coniferous wood) ; *myrosin*, or myronate of potash, $KC_{10}H_{18}NS_2O_{10}$ (seeds of Mustard) ; *salicin*, $C_{12}H_{18}O_7$ (in bark of Willows and Poplars) ; *gallotannin*, $C_{34}H_{28}O_{22}$ (in Oak-bark).

Though some of these substances (*e.g.* amygdalin and myrosin) contain nitrogen, it is more convenient to classify them with the more numerous non-nitrogenous glucosides.

4. *Fats and Fixed Oils :* these substances, as they occur in the seeds and fruits of plants, are mixtures of free fatty acids with glycerin-compounds (glycerides) of fatty acids ; thus palm-oil is a mixture of palmitic and oleic acids with their glycerides *palmitin*, $C_3H_5(C_{16}H_{31}O)_3O_3$, which is a solid fat, and *olein*, $C_3H_5(C_{18}H_{33}O)_3O_3$, which is a fluid fat or oil : olive-oil consists chiefly of olein with some palmitin : castor-oil, of ricinolein (the glyceride of ricinoleic acid) and stearin (the glyceride of stearic acid): linseed-oil, of linolein (the glyceride of linoleic acid) and palmitin.

5. *Essential or Volatile Oils :* these substances occur in various parts of

plants (flowers, fruit, etc.), and it is to them that the odours of plants are chiefly due. They usually consist of a mixture of oxygenated compounds with hydrocarbons of either the formula $C_{10}H_{16}$ (*terpenes*) or $C_{15}H_{24}$: many of the oxygenated compounds are solids held in solution in the liquid hydrocarbon; thus, *turpentine* (from Conifers) is a solution of *resin* (or abietic anhydride, $C_{44}H_{62}O_4$) in the terpene called *terebene*; camphor-oil consists of camphor ($C_{10}H_{16}O$), a solid substance, dissolved in a terpene; oil of cloves consists chiefly of *eugenol* ($C_{10}H_{12}O_2$) with a hydrocarbon $C_{15}H_{24}$. Some essential oils consist simply of a single substance the composition of which is various; thus, oil of bitter almonds is an oxygenated substance, C_7H_6O (benzoic aldehyde); oil of mustard is a sulphur-containing nitrogenous substance, C_3H_5,NCS (allylic isothiocyanate).

Allied to these hydrocarbons are the solid substances *caoutchouc* and *gutta-percha* which occur in milky latex: they have the composition $n(C_5H_8)$.

The organic compounds can for the most part be resolved into volatile products—chiefly carbonic acid, water, and nitrogen—by exposure to great heat with free access of air, that is, by combustion. The inorganic residue is a white, or, if the combustion is imperfect, a grey powder, the *ash.*

As the result of chemical processes attending the combustion, the sulphur and phosphorus previously contained in the organic compounds appear as sulphates and phosphates in the ash, and the carbonic acid formed during combustion combines with some of the inorganic substances. These, therefore, must not be included in an accurate estimate of the constituents of the ash.

The ash usually constitutes but a small percentage of the whole dry solid of the plant. The amount of ash increases with the age of the plant, or of any part of it, inasmuch as there is no appreciable excretion by the plant of the mineral substances absorbed. The percentage of ash in the dry solid of the plant, or of any organ, may vary widely at different times. The following analyses of various portions of plants will give an idea of its amount and composition:—

1000 PARTS OF DRY SOLID MATTER CONTAIN:

	Ash.	Potash.	Soda.	Lime.	Magnesia.	Ferric Oxide.	Phosphoric Acid.	Sulphuric Acid.	Silicia.	Chlorine.
Clover, in bloom	68·3	21·96	1·39	24·06	7·44	0·72	6·74	2·06	1·62	2·66
Wheat, grain .	19·7	6·14	0·44	0·66	2·36	0·26	9·26	0·07	0·42	0·04
Wheat, straw .	53·7	7·33	0·74	3·09	1·33	0·33	2·58	1·32	36·25	0·90
Potato tubers .	37·7	22·76	0·99	0·97	1·77	0·45	6·53	2·45	0·80	1·17
Apples . . .	14·4	5·14	3·76	0.59	1·26	0·20	1·96	0·88	0·62	—
Peas (the seed)	27·3	11·41	0·26	1·36	2·17	0·16	9·95	0·95	0·24	0·42

2. *The Food of Plants.* The constituents of the ash do not form a merely accidental mixture; it has been proved by experiment that certain inorganic compounds are absolutely necessary to the life of the plant. Those chemical elements which the plant requires for its nutrition, and which must therefore be regarded as part of its food, are:—

I. Non-metallic Elements:—Carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, and perhaps chlorine. It must, however, be clearly understood that all these elements also exist in the plant to some extent as inorganic compounds, carbonates, nitrates, phosphates, sulphates, of the metals mentioned below.

II. Metallic Elements:—Potassium, calcium, magnesium, iron.

Besides these we find in the ash of many plants—though they cannot be regarded as essential to nutrition—the following elements: sodium, lithium, manganese, silicon, iodine, bromine, and in rare cases, also aluminium, copper, zinc, cobalt, nickel, strontium, and barium. Fluorine must also exist in vegetables, for it is found in a perceptible quantity in the dentine of animals which feed directly or indirectly on vegetables.

The essential elements of the food will now be severally discussed.

Carbon. Plants which possess chlorophyll obtain their carbon mainly from the air (or, in the case of submerged plants, from the water) in the form of carbon dioxide. The absorption of carbon dioxide is, however, limited to those cells which actually contain chlorophyll, and it can only go on even in those cells so long as they are exposed to sufficiently intense light.

Although plants possessing chlorophyll can and do use carbon dioxide as carbonaceous food, yet there is reason to believe that they may supplement this by absorbing more complex carbon-compounds from the soil by their roots. Thus, a remarkable case of symbiosis (see p. 273), has been observed in various plants (especially trees belonging to Corylaceæ and Fagaceæ): the absorbent region of the roots is more or less closely covered by a felt-work of fungus-mycelium, the whole structure being termed *mycorhiza*: it is suggested, and the suggestion is based principally on the fact that the development of the mycorhiza is the more marked the richer the soil in decomposing organic matter (humus), that the fungus promotes the absorption of the organic matter by the roots of the tree. In certain other cases (*e.g.* Drosera, Dionæa, Utricularia, etc.), green plants are provided with a special mechanism, in the form of modified leaves, for obtaining a supply of organic carbon-compounds. Such plants are said to be *carnivorous.* The case of Drosera may be selected for illustration. The upper surface and the margin of a leaf of this plant bears numerous glandular appendages, the tentacles (see Fig. 42, p. 66). The glands at the ends of the tentacles continually excrete a viscid liquid. When an insect comes into contact with one of the marginal glands, it sticks to it; this stimulates the tentacle, and it moves, curving inwards to the centre of the leaf, and gradually the other marginal tentacles incurve over the insect (Fig. 42 *B*). The glands then secrete an acid liquid containing a digestive ferment which acts upon and dissolves the soft parts of the insect, and the products of this digestion are absorbed.

Plants which do not possess chlorophyll are incapable of using carbon dioxide as carbonaceous food, but require more complex carbon-compounds. Such plants are, all Fungi, and among the higher plants, Cuscuta (Dodder), Orobanche (Broomrape), Neottia, etc., though in some of these latter, a small, but altogether insignificant quantity of chlorophyll has been detected. These plants absorb the complex carbon-compounds which they require, either from living animals and plants, or from the decaying remains of animals and plants: in the former case they are termed *parasites*, in the latter *saprophytes.*

The most common parasites are those which are nourished by other plants, termed *hosts*, and each parasite has its own peculiar host, and possess peculiar root-like organs, the *haustoria* (see p. 66), by which they are attached to the host and absorb their nutriment. They frequently have a prejudicial effect upon the host, and sometimes cause malformations, such, for instance, as the "witches' brooms" in the Silver Fir, which are produced by a parasitic rust-fungus, the *Æcidium elatinum.* Less common are parasites on animals, such as the Schizomycetes (Bacteria, etc.), which cause various diseases, and other Fungi, like Entomophthora, which is parasitic on flies, and Cordyceps, which is parasitic on caterpillars.

Some of these parasites, Cordyceps for instance, can live saprophytically to some extent; these are potential saprophytes. On the other hand, there are potential parasites, that is, plants which can live almost as well parasitically as saprophytically, such as *Agaricus melleus*, which grows equally on living trees and on dead logs.

It is remarkable that certain plants which possess chlorophyll are nevertheless parasitic in habit; for instance, Viscum (the Mistletoe) which is parasitic on various trees, Rhinanthus (the Rattle) and other Scrophulariaceæ, also Thesium (Bastard Toad-flax), which are attached to the roots of other plants by their haustoria. The nutritive processes of these green parasites are not yet fully understood, but it seems probable that they absorb from their hosts the substances which they should normally obtain from the soil, though in a somewhat modified form.

The great majority of the saprophytes are Fungi, such as the various Agarics which grow in the soil of woods (humus) which is formed by decayed leaves and is rich in organic matter; the Moulds and Yeasts which grow in saccharine juices, or fruits, etc.; and Saprolegnia which attacks the corpses of animals. Some of these Fungi, notably the Yeasts and the various kinds of Bacteria (Schizomycetes), are peculiar in that they not only decompose the amount of organic substance which they require for their nutrition, but they give rise to widespread decompositions which are known as fermentation and putrefaction. Amongst the higher plants there are many saprophytes which grow in soils rich in humus: they may be almost destitute of chlorophyll (*e.g.* Monotropa; Neottia and some other Orchids): or they may possess it in considerable quantity (*e.g.* some Orchids; Pyrola; Ericaceæ; Diapensiaceæ), in which case they are probably only partially saprophytic; plants of this kind grow mostly in the leaf-soil of forests, or in peat on moors.

Hydrogen. The hydrogen of the plant is mainly absorbed in the form of water (H_2O), but it may also be absorbed in combination with nitrogen as ammonia-compounds (NH_3), and also in combination with carbon when complex carbon-compounds are absorbed by the plant.

Oxygen is absorbed in combination with carbon, as CO_2, and with hydrogen, as H_2O, and in many of the inorganic salts of the food, such as sulphates, phosphates and nitrates, as well as in more complex carbon-compounds. Oxygen is also absorbed uncombined, in connexion with the catabolic processes, in respiration.

Nitrogen, which is an essential constituent of proteid substances, is only exceptionally assimilated in the free form; although it is present in large quantities in the atmosphere, a plant perishes if the soil in which it grows contains no compounds of nitrogen. Nitrates and compounds of ammonia are widely distributed, and it is in this form that nitrogen is mainly taken up by plants; it seems probable that plants possessing chlorophyll absorb their nitrogen in the form of nitrates only.

Although it is usual to manure green crops with ammonia-compounds (*e.g.* sulphate of ammonia), the nitrogen is, nevertheless, absorbed in the form of nitrates. For there exist in the soil certain Schizomycetes, termed *Nitrobacteria*, which oxidise the ammonia-compounds present to nitrites, and these again to nitrates. This oxidising process is termed *nitrification.*

Nitrogen may be also absorbed, at any rate, by parasites, saprophytes, and carnivorous plants, in the form of nitrogenous carbon-compounds (see pp. 710, 692).

Although it is generally true that plants cannot assimilate uncombined nitrogen, nevertheless certain plants (Papilioneæ, such as Peas, Beans, etc.) will grow and flourish in a soil from which all traces of nitrogen-compounds have been carefully removed. The nature of the means by which this result is attained is not yet completely determined, but the principal facts are briefly as follows. In the first place, the roots of these papilionaceous plants have been found to bear peculiar gall-like outgrowths termed *tubercles*, which seem to be more numerous and larger the smaller the proportion of combined nitrogen contained in the soil. The tubercles are the result of the attack of a fungus which penetrates into the root through the root-hairs. The green plant and the fungus appear to exist in a state of symbiosis (p. 273), as in the case of the mycorhiza already mentioned, with the result that the green plant is adequately supplied with combined nitrogen although growing in a soil from which such compounds are originally absent. In explanation of these facts there can, first, be no doubt that the supply of combined nitrogen obtained by the green plant is ultimately derived from the free nitrogen of the atmosphere; and, secondly, that the supply is not obtained from the atmosphere directly by the leaves, but indirectly by the roots through the soil. Nor can there be much doubt that the tubercles are associated with the process of the assimilation of the free nitrogen: but it is a question whether this process takes place in the tubercle itself; or whether it is not carried on in the soil by a Schizomycete, which may either be derived from the tubercles, or be an independent organism. It seems probable that the latter suggestion is nearer the truth. It is, in fact, known that a bacterioid organism exists in the soil having the property of forming nitrogenous compounds from free nitrogen in the presence of non-nitrogenous organic substance (*e.g.* glucose). It may be that the development of this organism is especially favoured by the presence of the tubercular roots of the Papilioneæ in the soil, and that the nitrogenous substances which it produces are absorbed by the roots after having undergone nitrification (see p. 712).

The tubercles are structures formed by the hypertrophy of the cortex of the root, resulting from the attack of the fungus at various points: their cells are rich in sugar and starch: the branches of the mycelium penetrate most of the cells, and there bud off innumerable gemmules (sometimes called bacterioids). The tubercle eventually becomes disorganised; the gemmules are then set free into the soil, and are doubtless the means by which other roots become attacked by the fungus.

Sulphur, which is a constituent of proteids and a few other substances occurring in plants, such as oil of Mustard, is derived from the sulphates of the soil.

Phosphorus is absorbed from the soil in the form of phosphates, and enters into the composition of some of the proteid substances; phosphates constitute a large proportion of the ash of seeds.

As regards *Chlorine*, it has been experimentally proved so far to be indispensable in the case of one plant only, the Buckwheat (*Polygonum Fagopyrum*).

Iron, though it is met with in very small quantities, is absolutely necessary for the formation of chlorophyll. The leaves produced by plants which are not supplied with iron during their growth, are white so soon as their own store of iron is exhausted; these leaves, which are said to be *chlorotic*, become green in consequence of the formation of chlorophyll if the soil be supplied with iron, or even if their surface is washed with a very weak solution of iron.

Potassium is found in plants in the form of salts combined with various organic acids, as tartaric acid, malic acid, and oxalic acid. Unless the soil contains potassium-compounds, the assimilation of carbon dioxide by plants possessing chlorophyll does not go on, as is shown by the fact that, under these circumstances, the plant does not increase in dry weight. Potassium-salts are especially abundant in those parts of the plant which are rich in carbohydrates such as starch and sugar, as in potatoes, beet-roots, and fruits.

Calcium and *Magnesium* have been shown to be necessary to the normal development of plants: they are absorbed as nitrates, phosphates and sulphates, and thus serve as bases for the absorption of these other important elements. Little is known as to their direct use: they may be of importance in neutralising the organic acids (especially oxalic) formed in the plant; and calcium, at least, is of importance in connexion with the distribution of carbohydrates in the plant. They occur in the plant as salts of lime and magnesia in combination with both organic and inorganic acids.

It has been discovered by experimental cultures, that a plant can be perfectly nourished if it is supplied with all those elementary substances which have been enumerated as essential. This might be done, for instance, by growing it in a watery solution of either of the two following groups of chemical compounds:

1.

Calcium nitrate
Potassium nitrate
Potassium superphosphate
Magnesium sulphate
Ferrous phosphate
Sodium chloride.

2.

Calcium nitrate
Ammonium nitrate
Potassium sulphate
Magnesium phosphate
Ferrous chloride.

In these two mixtures, as well as in others of the same acids and bases which might be formulated, all the essential elements are included in forms suitable for absorption; the proportion of mixed salts should not, however, exceed about ·3% by weight of the liquid.

FIG. 471.—Water-cultures of Buckwheat (after Nobbe).

No. 1. Plant grown in normal solution.
,, 2. ,, ,, ,, ,, without potassium.
,, 3. ,, ,, ,, ,, with sodium-salts instead of potassium.
,, 4. ,, ,, ,, ,, without calcium.
,, 5. ,, ,, ,, ,, without nitrates or salts of ammonia.

This method of experimental culture, which is known as *water-culture*, has been of the greatest service in determining which are the essential mineral elements of the food, and of ascertaining the physiological significance of these elements in the metabolism of the plant.

The following is a brief account of the non-essential mineral constituents of the food.

Silicon, is absorbed from the soil as silica (SiO_2) or as silicates. It cannot be regarded as of nutritive importance, since plants which are usually rich in silica can be brought to an apparently normal development under conditions which render the absorption of silica impossible. It is usually deposited it the cell-walls, as in Diatoms, Equisetum, many Grasses, etc.

Iodine and *Bromine* are found in the many marine plants, especially in Algæ, and are prepared from them; it is not known that they are of any value in the economy of the plant.

Sodium, being universally distributed, is found in plants.

Lithium occurs in the ash of several plants, particularly in Tobacco.

Zinc, Copper, and other metals, though they are not commonly present in the ash of plants, are nevertheless taken up by plants from soils which are rich in them; from this it appears that plants may absorb substances which are not necessary and may be even injurious.

3. *Anabolism.* Under this term are included all the chemical processes going on in the plant which lead to the formation of complex substances from simpler ones (p. 669). Of these, those which are undergone by the food of the plant constitute *assimilation.*

In the case of plants which contain chlorophyll, the first step in the assimilation of the food is the construction of a carbon-molecule which contains hydrogen and oxygen. The process may be represented by the following equation

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

That some process of the kind takes place is proved by the fact that when green plants are placed under the necessary conditions, that is, when they are supplied with carbon dioxide, with water and with salts from the soil, and are exposed to light, they gain in weight in consequence of an increase in the amount of their dry organic substance, and they give off oxygen. Moreover, the volume of the free oxygen evolved is actually equal to that of the carbon dioxide absorbed, as indicated in the equation.

There are three points connected with the performance of this process which require special notice: the part played by the mineral food, the action of light, the function of chlorophyll.

With regard to the first point, it appears that the process in question cannot be performed unless potassium-salts are supplied to the plant. There is no reason to believe that this metal takes any direct part in the process; but it has an indirect, though none the less well-marked effect upon it (see p. 714).

The importance of exposure to light is briefly this. The chemical process represented in the foregoing equation is one which involves the doing of work; for, from the simple and stable molecules, CO_2 and H_2O, a more complex and less stable molecule CH_2O is produced. Work cannot be done without energy, and the plant cannot evolve in itself the energy necessary. It avails itself, therefore, of the kinetic or radiant energy of the sun's rays. Hence the importance of exposure to light is that the plant, by absorbing the light-rays, obtains the energy required for the chemical work which has to be done.

Next, as to the function of chlorophyll. The function of chlorophyll is to serve as the means by which the rays of light are absorbed, and their energy made available for the performance of the chemical work by the protoplasm with which the chlorophyll is associated. When light which has passed through a solution of chlorophyll is examined with a spectroscope, the spectrum is seen to present certain dark bands, known as absorption-bands, in the red, yellow, green, blue, and violet, the band in the red being the most conspicuous. These bands indicate that certain of the rays of the solar spectrum do not pass through the chlorophyll, but are arrested and converted into another form of energy. It is this energy which, in the living plant, the chlorophyll places at the disposal of the protoplasm for the construction of an organic molecule out of carbon dioxide and water, as expressed in the foregoing equation. Protoplasm without chlorophyll is incapable of making use of the kinetic energy of the rays of light for the performance of this chemical work.

The product of this process of carbon-assimilation is (as indicated in the foregoing equation) a non-nitrogenous organic substance having the composition of a carbohydrate. A leaf which is actively assimilating carbon under the influence of light is generally found to contain relatively large quantities of carbohydrate, in the form either of sugar or starch.

The performance of this process can be readily demonstrated. If a water-plant (*e.g.* a leaf of *Potamogeton natans*, or a portion of the shoot of *Elodea canadensis*) be placed in water which holds carbon dioxide in solution, and be exposed to sunshine, it will be seen that from the cut surface of the leaf or stem bubbles of gas are given off at regular intervals (Fig. 475). These consist of oxygen.

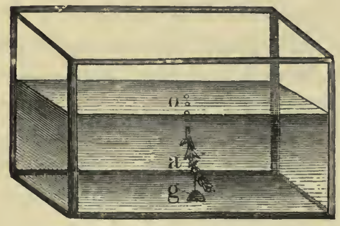

FIG. 475.—Evolution of oxygen from a water-plant (*Elodea canadensis*): *a* the cut stem; *g* a weight that keeps the stem in its place; *o* the gas-bubbles rising from the cut surface.

The relation of light and of chlorophyll to the evolution of oxygen by a green plant is strikingly illustrated by means of an aerobic Bacterium (*Bacterium Termo*), which is highly sensitive to the presence of oxygen. If a filamentous Alga be placed under a cover-slip on a slide under the microscope, in water containing numerous Bacteria, the Bacteria will be seen to collect along the filament, attracted by the free oxygen which is being evolved. The same preparation will serve to show which are the rays of light most active in the process. If, instead of ordinary white light, a spectrum be reflected by the mirror of the microscope on to the slide bearing the Alga and the Bacteria, the Bacteria will not be distributed uniformly along the filament, as in white light, but will aggregate at certain points (more especially in the red and in the blue), which correspond with the principal absorption-bands of the chlorophyll-spectrum.

The relation of light and of chlorophyll to the formation of organic substance by a green plant can be demonstrated by the starch-method. For instance, if a leaf of a starch-forming plant, which has been exposed to bright light for some hours, be removed, decolourised by alcohol and tested with iodine, it will assume a dark blue colour, showing an abundant accumulation of starch. If a leaf, still on the plant, be exposed, not to white light, but to a spectrum, the starch will be found to have accumulated in these portions of the leaf upon which have fallen the rays of light which correspond to the principal absorption-bands of the chlorophyll-spectrum.

The process under consideration is one of fundamental importance. It is the great process in nature by which organic substance is constructed, and in which kinetic energy absorbed from without is converted into the potential energy of chemical combination. For the energy of the rays of light which is used in the construction of the organic substance is not lost, but is simply converted into another form, and it can be recovered by undoing the chemical work which has been performed. When a piece of wood or of coal is burned, the heat and the light which are given out represent the energy which was used by the plant in constructing the organic substance of which the wood and the coal consist, and which exists in them as the potential energy of chemical combination. To put the matter more definitely; if the organic substance which has been formed by a green plant under the influence of light according to the equation

$$CO_2 + H_2O = CH_2O + O_2$$

be burned, the chemical process is precisely reversed, according to the equation

$$CH_2O + O_2 = CO_2 + H_2O,$$

and precisely the same amount of energy is evolved in the kinetic state in the second process, as was stored up in the potential state in the first.

It is, generally speaking, only plants possessing chlorophyll which can produce organic substance. Inasmuch, therefore, as organisms, whether plants or animals, which do not possess chlorophyll require for their nutrition more or less complex organic substances, they are entirely dependent for their food upon organisms which do possess chlorophyll.

To this general rule exceptions are offered by certain Schizomycetes. Thus some Bacteria (*e.g. B. photometricum*) contain a purple colouring-matter (bacterio-purpurin), but no chlorophyll: they are, however, capable of forming organic matter with evolution of oxygen when exposed to light; the bacterio-purpurin appears to perform essentially the same physical function as chlorophyll, though it does not absorb the same rays of light. Again, other Bacteria, such as the Sulphur-bacteria (*Sulphobacteria*), the Iron-bacteria (*Ferrobacteria*), and the nitrifying Bacteria (*Nitrobacteria*) produce organic substance, although they possess no chlorophyll, and do so quite independently of light, the necessary energy being obtained in other ways (see p. 731).

This process is also of great importance in another direction. All living organisms, speaking generally, absorb free oxygen and evolve carbon dioxide in respiration. Those organisms which possess chlorophyll prevent the excessive accumulation of carbon dioxide in the atmosphere, and keep up the supply of free oxygen, in that, under the influence of light, they absorb the former gas from the air, and replace it by an equal volume of the latter.

The characteristic difference between the anabolic capacity of plants which do and of those which do not possess chlorophyll is then this, that the former can produce, from carbon dioxide and water, assimilable or plastic substances containing the elements C, H, and O, whereas the latter cannot produce these, but must be supplied with them as food. From this point onwards the anabolic processes in the two cases are, as far as is known, identical. From the simpler plastic substances containing C, H, and O, whether they have been formed from CO_2 and H_2O in the one case, or have been absorbed as organic food from without in the other, other more complex substances such as sugar, etc., are formed, probably by the polymerisation or condensation of the simpler molecules. Further, the nitrogen of the food, absorbed either as nitrates or salts of ammonia, is worked into the anabolic processes, so that nitrogenous organic substance is produced. Probably the first formed nitrogenous substances are comparatively simple crystallisable substances, such as asparagin and leucin, which belong chemically to the amides (see p. 707). The next step is doubtless the formation of those more complex nitrogenous substances, the proteids, and here sulphur, and phosphorus in some cases, is introduced into the molecule; and finally the series of assimilatory processes concludes with the formation of molecules of protoplasm.

Comparatively little is known as to the details of nitrogenous anabolism; but there is evidence to show that, in green plants, the assimilation of the nitrates (see p. 712), and probably also of the sulphates and phosphates, of the food can only go on in the presence of light; and when it is borne in mind that these salts are, like carbon dioxide, highly oxidised substances, it is not surprising that the conditions for the reducing process in the one case should obtain also in the others. And further, there is evidence to show that the next step in nitrogenous anabolism, the production of proteids from amides, is also dependent not merely upon exposure to light, but upon the coincidence of this with the other conditions necessary to the assimilatory function. For instance, asparagin (whether formed anabolically or catabolically) will accumulate in a shoot kept in the dark, although carbohydrates may also be abundantly present: it will also accumulate if the shoot be exposed to light, but in an atmosphere deprived of CO_2: whereas it will not accumulate in a shoot exposed to light under conditions which enable the shoot to assimilate carbon dioxide. How and where this formation of proteids from amides takes place is not accurately known. But there is some evidence that, for instance, in the leaf of a vascular plant, the process is carried on in the companion-cells of the sieve-tissue or their physiological equivalents. It appears that the amides formed in the green assimilating cells are collected into this tissue, and there undergo further anabolism into the proteids to be found in the sieve-tubes.

Inasmuch as plants destitute of chlorophyll absorb their nitrogenous food in the form of ammonia-compounds (see p. 712) or of organic nitrogen-compounds, it is intelligible that exposure to light is not an essential condition of their nitrogenous assimilation.

These various assimilatory processes are not, however, carried on simultaneously with equal activity. In plants which contain chlorophyll, when under conditions favourable for carbon-assimilation, the construction of non-nitrogenous organic substance from CO_2 and H_2O appears to be the most active process, for an accumulation of non-nitrogenous organic substance can be detected in the green parts of these plants when assimilation is being carried on. Most commonly this excess of non-nitrogenous organic substance is accumulated in the form of starch-granules which are formed in the chloroplastids; less commonly in the form of sugar which is held in solution in the cell-sap (*e.g.* leaves of Onion). This excess of non-nitrogenous organic substance in the green parts soon disappears, however, when, by withdrawal from the influence of light, its further formation is arrested. For instance, if a plant which has been exposed to light and whose leaves are rich in starch, be placed in the dark for some hours, the starch will then be found to have almost or entirely disappeared.

The organic substance resulting from the anabolism of the plant, is partly used in the growth of the plant, in forming new protoplasm, cell-walls, etc., and is partly stored up, in various organs, in the form of reserve materials which serve either for the growth of the plant itself at a subsequent period (roots, tubers, etc.), or for the nutrition of new individuals in the early stages of their growth (spores, seeds, etc.).

4. *Catabolism.* Under this term are included all the chemical processes going on in the plant which lead to the formation of simple substances from more complex ones.

The chief physiological importance of the catabolic processes is this: that, inasmuch as they consist in the decomposition of relatively complex and unstable substances into others which are relatively simple and stable, they necessarily involve a conversion of potential into kinetic energy; and it is by means of the kinetic energy so evolved that the plant exhibits those phenomena, such as growth, movement, etc., which characterise it as a living organism. The degree of activity of life depends directly upon the degree of catabolic activity; when catabolism ceases, life ceases; the organism is dead. A good illustration of this is afforded by the scarcely perceptible catabolism of seeds, bulbs, etc., when quiescent, and their very active catabolism when they begin to germinate.

The catabolic processes of the plant are carried on either by the living protoplasm itself, or by means of certain substances formed by the protoplasm, which are termed *unorganised ferments* or *enzymes*.

The catabolic processes carried on by the protoplasm are mainly such as depend upon the absorption of free oxygen from without, and are accompanied by an evolution of carbon dioxide; in fact this gaseous interchange between the plant and its environment, termed *Respiration*, is the external manifestation of the performance of these catabolic processes. The seat of these processes is the protoplasm, and it is mainly the molecules of protoplasm that are decomposed; in other words, just as the construction of the protoplasm-molecule is the ultimate result of anabolism, so the decomposition of the protoplasm-molecule is the central fact of catabolism.

The significance of the absorption of free oxygen in connexion with catabolism appears to be this: the chemical decompositions which constitute catabolism involve a certain expenditure of energy, though the amount thus expended is very much less than the amount evolved by the decompositions; the smaller, then, the the amount of the energy expended, the greater will be the amount of available kinetic energy in the plant: now the entrance of free oxygen into the decompositions facilitates their performance, so that, under these circumstances, the largest amount of kinetic energy is evolved at the smallest initial expenditure.

The reason, then, why most plants die when they are deprived of free oxygen, is that they are unable to carry on, under these circumstances, those catabolic processes by which the kinetic energy essential to the maintenance of life is evolved; just as a fire goes out, that is the oxidation of the coal stops, under the same conditions.

Though it may be generally stated that living plants at all times absorb free oxygen, and that the maintenance of life depends upon a constant absorption of free oxygen, yet there are exceptions. There are, for instance, certain Fungi, such as Yeast and Bacteria, which can live in the absence of free oxygen. They are unable, under these conditions, to carry on what may be termed the normal oxidative catabolic processes; but they carry on other processes of decomposition into which free oxygen does not enter, provided that suitable material is accessible; the processes are termed *fermentations.* Thus, Bacteria cause putrefaction and other similar fermentations in the most various organic substances with which they happen to come into contact. Similarly Yeast is the cause of the alcoholic fermentation of sugar, which may be represented by the equation

$$C_6H_{12}O_6 = 2C_2H_6O + 2CO_2.$$

These fermentative catabolic processes involve, like the oxidative catabolic processes, an evolution of kinetic energy, but this is, generally speaking, attained by a greater initial expenditure. Yeast, for instance, certainly thrives better when it can obtain free oxygen than when it cannot; but many of the Bacteria have become so completely adapted to a life based upon fermentative catabolism, that they die if they come into relation with free oxygen (*anaerobia*).

Yeast, Bacteria, and other plants which can excite fermentation are termed *organised ferments*, inasmuch as they are complete living organisms and as their power of exciting fermentation depends upon their being alive, in contradistinction to the unorganised ferments or enzymes already mentioned, which are not organisms, but simply chemical substances which may be prepared and kept under conditions which would be fatal to life. The peculiar properties of the unorganised ferments can, however, be very readily destroyed, as, for instance, by boiling or otherwise heating.

The chief kinds of *enzymes* which have been found in plants are:—

1. Those that act on carbohydrates, converting the more complex and less soluble carbohydrates into others of simpler composition and greater solubility.

2. Those that act on fats, decomposing them into glycerin and fatty acid.

3. Those that act on glucosides, glucose being a constant product.

4. Those that act on the more complex and less soluble proteids, converting them into others which are more soluble and probably less complex, or decomposing them into non-proteid nitrogenous substances (amides, etc.).

The chemical action of some of these enzymes are illustrated by the following equations:—

1. Conversion of starch into sugar (*amylolytic* enzyme, commonly termed *diastase*):—

Starch. Maltose. Dextrin.

$$3\,(C_6H_{10}O_5)+H_2O=C_{12}H_{22}O_{11}+C_6H_{10}O_5$$

2. Conversion of cane-sugar into grape-sugar (invert enzyme):—

Cane-sugar. Dextrose. Lævulose.

$$C_{12}H_{22}O_{11}+H_2O=C_6H_{12}O_6+C_6H_{12}O_6$$

3. Action of fat-enzyme:—

Oleïn. Oleic acid. Glycerin.

$$C_{57}H_{104}O_6+3H_2O=3C_{18}H_{34}O_2+C_3H_8O_3$$

4. Action of glucoside-enzyme; the instance taken is the decomposition of the glucoside amygdalin in the Bitter Almond by the ferment termed *synaptase* or *emulsin*:—

Amygdalin. Oil of bitter almonds. Prussic acid. Glucose.

$$C_{20}H_{27}NO_{11}+2H_2O \quad = \quad C_7H_6O \quad + \quad HCN \quad + \quad 2(C_6H_{12}O_6)$$

It will be noted that, in every case, the action of the ferment involves the taking up of one or more molecules of water.

The action of the enzymes which act on proteids (*proteolytic* enzymes) cannot be represented by equations, inasmuch as no formulæ for the various proteids have at present been arrived at. It may be generally stated that their effect is, like those of the other forms, to induce decomposition with the assumption of water. The proteolytic ferments, acting some in an acid medium, others in an alkaline, convert the more complex proteids, such as globulins, into the simpler peptone; and further cause the decomposition of peptone into amides, such as asparagin, leucin, and tyrosin.

The chief importance of the unorganised ferments in the economy of the plant is that by their means the reserve materials, which are accumulated to such a large extent in the form of substances, such as starch, fat, cellulose, proteids of aleurongrains, which are either not soluble in water, or if soluble are only slightly diffusible, are converted into substances, such as amides and certain sugars, which are both readily soluble and diffusible, and which can therefore travel osmotically from one part to another. For instance, as mentioned above, the excess of carbohydrate formed in the leaves when they are actively assimilating, is commonly stored up in the form of starch. This carbohydrate is eventually conveyed to other parts of the plant; but, since starch is insoluble, it cannot be conveyed in that form; it is, in fact, converted into maltose by an amylolytic ferment present in the leaves, and it is in this form that non-nitrogenous organic substance is conveyed away from the leaf where it has been produced. Other striking illustrations of the importance of ferment-action are to be found in the chemical changes going on in germinating seeds, bulbs, tubers, etc. When a starchy seed, or a starchy tuber like the potato, germinates, the starch-grains are gradually dissolved, the starch being converted into maltose. When the tuber of the Dahlia or Artichoke, which contains inulin as the non-nitrogenous reserve material, germinates, the inulin disappears and is gradually replaced by grape-sugar. When an oily seed germinates, the oil-drops become less and less apparent, as the oil is gradually decomposed by ferment-action into glycerin and fatty acids; the next step is the formation of carbohydrate (sugar or starch), probably from the products of the decomposition of the oil, a process which involves the absorption and fixation of oxygen, since carbohydrates contain a higher percentage of oxygen than does any form of fat or oil; and then, finally, any starch so formed is converted into sugar. Similarly, the aleuron-grains in a germinating seed gradually disappear, the indiffusible proteids composing them being decomposed by the action of a proteolytic enzyme into peptone, and then into amides, in which form they are conveyed osmotically to the growing embryo. Finally, it is obvious that the indiffusible proteids which are conveyed from part to part in the sieve-tissue of vascular plants (see p. 705) must eventually be distributed osmotically in the form of diffusible compounds, probably amides, to the adjacent parenchymatous tissues, and it is probable, though not yet ascertained, that here again a proteolytic enzyme is involved.

It is worthy of note that the chemical decompositions effected by the agency of the enzymes do not involve either an absorption of oxygen or an evolution of carbon dioxide, whereas this is the case in the decompositions effected by the agency of living protoplasm. But to the latter general rule there are some exceptions. Thus, it has been observed that succulent plants, such as Cactaceæ, Crassulaceæ, etc., absorb free oxygen without exhaling any carbon dioxide; but it has further been found that, under these circumstances, there is an accumulation of organic acids (especially malic) in the tissues. The explanation is this: that, owing to some peculiarity in their catabolic process—possibly to the imperfect aeration of their tissues—instead of producing the very simple substance carbonic acid, which would be exhaled in the form of the gas CO_2, these plants produce more complex, less highly-oxidised carbon-acids, which are not volatile at ordinary temperatures, and which therefore remain in the cells of the plant: these acids (at least malic acid) subsequently undergo decomposition under the influence of light with the formation of carbohydrates. Again, the decompositions effected by organised ferments (*e.g.* alcoholic fermentation) commonly involve an evolution of carbon dioxide without any corresponding absorption of oxygen.

Respiration. This term is applied to the gaseous interchange, consisting in the absorption of free oxygen and the evolution of carbon dioxide, which takes place (with but few exceptions) between the living plant and the atmosphere, and which may be regarded as the external expression of the oxidative catabolic process going on in the tissue of the plant. This gaseous interchange goes on over the whole surface of the body; but in those parts which possess stomata or lenticels, it is mainly conducted through these apertures.

Respiration seems to be somewhat diminished under the influence of bright light; but its activity is promoted by a rising temperature, and to some extent by greater moistness of the air. The relation to temperature is such that respiration takes place at temperatures even slightly below 0°C.; that it increases in intensity with a rise of temperature, but in greater proportion, up to an optimum of 40°–45°; and then sinks as the temperature further rises until the fatal degree is reached.

The relation of the volume of the gases absorbed and evolved in respiration, that is, of oxygen and carbon dioxide, is a matter of importance. It may be generally stated that the relation is definite and constant for any given plant, or for any part of it, at a given stage of development, all other conditions being constant: the proportion $\frac{CO^2}{O}$ may be unity, or less or more than unity, according to the nature of the plant under experiment, and is not affected either by temperature or by light.

As illustrating the possible extremes of variation in the proportion, the following cases may be mentioned. In succulent plants, when in darkness, (see p. 725) oxygen is absorbed, but no carbon dioxide is evolved: and on the other hand, when Yeast and Bacteria, or germinating seeds, or parts of plants (fruits, leaves, etc.), are kept in an atmosphere destitute of free oxygen, they evolve carbon dioxide: again, at periods, such as a certain stage in the germination of seeds, the opening of buds and flowers, when the activity of respiration is intense, the proportion $\frac{CO_2}{O}$ is at a maximum, though it rarely exceeds unity, that is, the evolution of CO_2 is relatively large; whereas during periods of more normal respiratory activity, the proportion of carbon dioxide evolved is smaller. The variations in the proportion $\frac{CO_2}{O}$ are the expression of the varying nature of the catabolic processes going on during different stages in the life of the plant or of any of its parts.

5. *The Products of Metabolism.* The relation between the anabolism and the catabolism of the plant may be generally stated thus, that the construction of organic substance in the former is greater than the decomposition of it in the latter, so that on the whole there is an accumulation of organic substance in the body of the plant. The organic substance is accumulated to some extent in the actual structure or fabric of the plant, as protoplasm and cell-wall, and to some extent in the form of compounds which may be present in some or all of the cells, but which do not constitute any portion of the fabric. These compounds may or may not be of nutritive value; in the former case they are termed *plastic products*, in the latter *waste-products*, of metabolism (see p. 670.)

The most important of the *plastic products* are enumerated below. They are all found accumulated as reserve materials in various parts of plants, though some of them (*e.g.* amides, glucose, maltose) are more especially the forms in which organic substance is distributed throughout the plant.

Non-nitrogenous reserve materials :—

- *a.* Carbohydrates ; in solid granules, starch ; in many seeds, and tubers,
    - in thickened cell-walls, cellulose ; as in Date-seed, Coffee-seed, Vegetable Ivory.
    - dissolved in cell-sap ; grape-sugar, as in the Onion and in fruits ; cane-sugar, as in the Sugar-cane and the Beetroot ; inulin, as in the Jerusalem Artichoke and Dahlia.
- *b.* Fats ; in drops in many seeds (Rape, Linseed, Castor-oil, Palm, etc.).

Nitrogenous reserve materials :—

- *a.* Proteids ; in solid granules (aleuron ; p. 112), in seeds, more especially oily seeds ; or in the cytoplasm (*e.g.* latex).
- *b.* Amides ; asparagin, etc., in solution in the cell-sap of bulbs, tubers, bulbous roots, etc.

With regard to the mode of formation of these substances, some of them are certainly produced both synthetically and analytically, that is, both in anabolism and in catabolism, whereas others are only produced in one or other of these ways.

Fats and Carbohydrates. There is some evidence that fats are formed in the catabolism of protoplasm : that is, that in the decomposition of the protoplasmic molecule, fat is frequently one of the products : there is also reason to believe that the purely reserve carbohydrates, starch, cane-sugar, and cellulose, have a similar origin. The other sugars (glucose, maltose) may be formed anabolically, but are also formed by enzymes from the reserve carbohydrates.

Organic acids. It is scarcely possible to make any general statement as to either the origin or the fate of these substances which are so largely present in plants. They are probably formed mainly by normal oxidative catabolic processes, but the formation of some of them (*e.g.* oxalic acid) is at the same time closely allied with certain anabolic processes in the plant: however, there is no doubt that they are not, as was formerly held, ever formed synthetically. The more complex acids may certainly be looked upon as plastic substances: for, in succulent plants (see p. 725) it has been found that the malic acid, which accumulates in the tissues during darkness, is decomposed by the green parts in the light, with evolution of oxygen and formation of less highly oxidised organic substance (carbohydrate). In fact, the process of assimilation of these acids is essentially the same as that of carbon dioxide, the only difference being that carbon dioxide is more highly oxidised than are these more complex acids, but the conditions of the process are identical in the two cases. These organic acids are of considerable physiological importance in effecting the decomposition of the salts (*e.g.* nitrates, sulphates, phosphates) absorbed from the soil.

Amides are formed both in anabolism (p. 720), and in catabolism (p. 725).

Proteids may all be formed in anabolism; and the simpler forms (peptones) in catabolism. It is a question whether or not the more complex proteids may not be formed by dissociation of the molecule of protoplasm.

The *waste-products* are most probably all formed as the result of catabolic processes; though their formation is often associated, both as to time and place, with active anabolism. They may be classified into nitrogenous and non-nitrogenous.

The principal nitrogenous waste-products appear to be the *alkaloids* (see p. 707). They are probably products of the nitrogenous catabolism of plants; and it is suggestive that they principally occur deposited in the cells of deciduous parts, such as leaves, seeds, bark, etc.

The principal non-nitrogenous waste-products are, water; free oxygen (green plants in light); carbon dioxide, and some other highly oxidised carbon-acids, such as the oxalic; resins and ethereal oils, tannins, aromatic substances, etc.

Of these waste-products, some are retained in the cells of the plant, whereas others are thrown off or *excreted.* The nitrogenous waste-products are deposited either in cells or in the laticiferous tissue: there is practically no excretion of such waste-products by plants. Similarly, those of the non-nitrogenous waste-products which are not gaseous at ordinary temperatures, are retained by the plant. For instance, oxalic acid is deposited in the form of crystals of calcium oxalate either in the cavities or in the walls of the cells (see pp. 108, 113): the crystals may have either six molecules of water of crystallisation, when they are quadratic; or two molecules, when they are prismatic (raphides). The resins and ethereal oils are usually excreted by the cells in which they are formed, into intercellular spaces (resin-ducts, oil-glands, see p. 138): the tannins are mostly stored in cells, dissolved in the cell-sap.

Some general idea may be formed as to the relation of these substances to the catabolic processes by a consideration of the origin of oxalic acid and of tannin in the plant: the matter has been more fully investigated with reference to these substances than to any others, and the results in these two cases correspond in a remarkable manner.

In the first place, both these substances are abundantly formed in connexion with active chemical change of the plastic substances (probably the nitrogenous) supplying the demands of a growing part: for instance they are abundant in seedlings, in developing shoots, roots, etc. This formation, which is quite independent of light, is distinguished as *primary*, and the calcium oxalate and the tannin thus formed remain permanently in the cells in which they are formed: the primary calcium oxalate is characterised by the prismatic form (raphides). A *secondary* formation of both these substances takes place in green parts of plants exposed to light, in leaves for instance: they are formed so abundantly under these circumstances that they must be continually transported (in solution by osmosis) from the seat of formation to other parts, for instance, from the leaves to the stem. This secondary formation is associated, not with the assimilation of carbon dioxide, but with the formation of nitrogenous organic substance (see p. 720): but though associated with this anabolic activity, the actual process of formation of these two substances is probably not synthetic, but analytic; it is a catabolic process which necessarily accompanies the anabolic.

The oxygen which is set free in connexion with the decomposition of CO_2 in the green parts under the influence of light, is exhaled in the gaseous form; this is also the case, for the most part, with the watery vapour and the carbon dioxide produced in catabolism. In some cases, however, some portion of the carbon dioxide forms calcium carbonate, which is either deposited in the solid form (*e.g.* cystoliths, see p. 108), or is excreted by means of the chalk-glands (p. 137).

In some cases, substances of nutritive value are excreted by plants, as for instance, the sugary liquid known as nectar by special glands, the nectaries (see p. 679), of flowers, and the digestive liquid poured out by the glands of the carnivorous plants. This loss of substance is, however, compensated for by the advantages gained by the excretion. The nectar attracts insects, and so ensures cross-fertilisation, and the excretion of the carnivorous plants results in the digestion of the entrapped insects (see p. 711).

The mechanism of *excretion* may be generally illustrated by reference to two cases: to the nectaries, and to the chalk-glands. The former afford an example of that mode of excretion in which the necessary force is supplied by the excreting cells themselves: the latter, of that mode in which the necessary force is derived from another source. Excretion by nectaries can be well observed in the case of *Fritillaria imperialis* (Fritillary, or Crown Imperial). At the base of each of the petals of the flower, there is an oval depression which is the gland or nectary and is seen to be occupied by a large drop of nectar. If the flower be cut off, and the drop be removed from the nectary by means of blotting-paper, it will be shortly replaced by a fresh drop. It is therefore clear that in this case the excretion of the liquid is effected, not by the root-pressure, for the flower is no longer in connexion with the root, but by the cells themselves. The mechanism of excretion seems to be this, that the cells of the nectary become turgid, and when a certain degree of turgidity has been attained, filtration under pressure (see p. 669) takes place, and liquid is pressed out. Excretion by chalk-glands can be well observed in some of the Saxifrages. The chalk-glands are here situated at the end of the finer vascular bundles round the margin of the leaves, each gland being at the bottom of a depression in the surface, and communicating with the surface by two or three water-stomata (see p. 157). So long as the leaf is in connexion with the rest of the plant, and provided that transpiration is not too active, drops of water holding chalk in solution are poured out by these glands on to the surface through the water-stomata. The excretion stops, however, directly the leaf is removed, or the stem is cut through. In this case the excretion clearly depends upon the root-pressure; the gland itself has no excreting power, but it simply accumulates the chalk which is then washed out by the current of water forced through the gland by the root-pressure.

6. *The Supply and the Expenditure of Energy.* It has been already insisted upon that a living organism must be supplied not only with matter, but also with energy. The principal sources of the supply of energy will now be briefly considered.

a. All plants absorb kinetic energy in the form of heat (see p. 671).

b. Plants which possess chlorophyll absorb kinetic energy in the form of light, the rays absorbed being those which correspond to the absorption-bands of the chlorophyll-spectrum (see pp. 674 and 717).

c. Plants which do not possess chlorophyll are unable to absorb kinetic energy in the form of light, but they obtain their supply in other ways. For instance, it has been pointed out (p. 711) that these plants require more or less complex carbon-compounds as food: the significance of this fact is not only that these plants are unable to produce these compounds for themselves from carbon dioxide and water, but further, that these compounds represent potential energy which, in the decomposition of these compounds in the body of the plant, is evolved in the kinetic form: hence these organic food-substances supply the plants not merely with matter, but also with energy.

Plants without chlorophyll also obtain energy by yet other means. For instance, when sugar is fermented by Yeast (see p. 723), there is a considerable evolution of energy, and this is the true significance of the process from the point of view of the Yeast-plant: similarly, Bacteria cause various putrefactive and other fermentations which are attended by an evolution of energy. In these cases it would appear that the plant avails itself of the kinetic energy evolved in the fermentative process.

A few cases have been investigated among Schizomycetes in which the supply of kinetic energy is obtained by oxidative processes: this occurs, for instance, in the case of the nitrifying organisms (*Nitrobacteria*) which oxidise ammonia compounds to nitrites, and nitrites to nitrates, in the soil: in the case of the *Sulphobacteria* which oxidise hydrogen sulphide (H_2S) with the formation of sulphates: and in the case of the *Ferrobacteria* which oxidise ferrous to ferric salts (see p. 719).

The energy obtained in any of these ways is of primary importance in the anabolism of the plant: it is concerned with the building up of more and more complex organic compounds and with the nutrition of the protoplasm; and in as far as these compounds, such as carbohydrates, proteids, etc., accumulate in the plant, in so far is potential energy accumulated likewise. But, inasmuch as the catabolic processes are at the same time in constant operation, there is going on in the plant a constant conversion of potential into kinetic energy, a considerable proportion of which is *dissipated* or lost to the plant.

Energy is most commonly dissipated in the form of heat, in a few cases in the form of light, and also commonly in the form of movement. The evolution of heat by plants is not usually sufficient to cause the temperature of the plant-body to be higher than that of the surrounding air. This is partly due to the fact that the catabolic processes of plants are not generally very active, and partly to the continual loss of heat by radiation and in connexion with transpiration. It is however easy, under appropriate conditions, to demonstrate the evolution of heat. If a quantity of seeds be made to germinate in a heap, they will be found to be distinctly warm (Fig. 476). This happens on a large scale in the process of malting barley. When a large quantity of barley-grains are germinating on a malting-floor, they become quite hot: they have, in fact, to be continually turned to prevent overheating. The conditions are here most favourable: for the catabolic processes are extremely active in germinating seeds, and there is but little loss of heat by radiation and transpiration. Similar observations may be made with opening flower-buds, the opening of the bud being also a period of great catabolic activity. In some cases, as in the Araceæ, where the inflorescence consists of a great number of flowers which open simultaneously, and which are protected by a large leaf, the spathe, a rise of temperature as much as 18° C. has been observed.

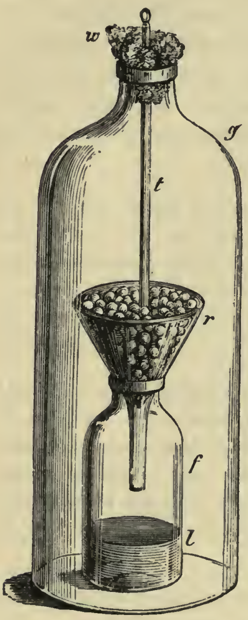

FIG. 476.—Apparatus for detecting the rise of temperature in small opening flowers or germinating seeds. The seeds are heaped as closely as possible in the funnel *r* which is inserted into the mouth of a bottle containing a solution of caustic potash. This absorbs the carbon dioxide produced by respiration. The whole is enclosed in a glass vessel, and a delicate thermometer is inserted through the cotton wool which closes the mouth. The bulb of the thermometer is plunged in among the seeds. The temperature in this apparatus will be higher than in another arranged in the same way for comparison, and in which the flowers or seeds are replaced by scraps of paper, etc.

The few plants in which an evolution of energy in the form of light has been clearly established are all Fungi. It is commonly termed *phosphorescence.* The so-called phosphorescence of decaying wood is due to the presence of the mycelium of *Agaricus melleus*, and that of putrifying meat and vegetables to Schizomycetes of the nature of Micrococci. Various other species of Agaricus have been found to be luminous.

Movement of some kind is manifested by all plants. All plants exhibit that slow movement which is termed growth: in many, there is a more or less well-marked movement of the protoplasm in the cell or cells of which the plant-body consists, which is known as *cyclosis*, *cir-*

culation, or *rotation*: some are capable of locomotion during the whole or a portion of their life, a peculiarity which is shared by many reproductive cells, such as zoospores and spermatozoids: in some cases, the floral or the foliage-leaves of the plant can perform movements, as the foliage-leaves of the Sensitive Plant, of the Telegraph-plant, of *Dionæa muscipula* (Venus Fly-trap), the stamens of Berberis and of the Cynareæ, or portions of leaves as the tentacles of Drosera (Sun-dew, see p. 711). These movements are considered in detail in the next chapter.

The connexion between these various forms of dissipation of energy and the catabolic processes, is clearly demonstrated by the fact that any change which prejudicially affects the activity of catabolism, similarly affects the dissipation of energy. For instance, in the absence of free oxygen, a condition which diminishes catabolic activity in most cases, germinating seeds or opening flowers cease to evolve heat; the luminous Fungi cease to emit light; growth, and the other more conspicuous movements are arrested: similar effects are produced by exposure to a low temperature.

The main facts of the metabolism of the plant may be clearly summed up in a general table of the income and expenditure, such as the following. It may be explained that in this table account is taken of only that portion of the water absorbed from without which actually enters into the metabolism; the remainder, which simply traverses the plant to be exhaled as vapour in transpiration, is not considered. Under the head of "incidental losses" are included the loss of organic substance connected with throwing off reproductive cells, such as spores and spermatozoids, or other reproductive organs such as seeds, bulbils, etc.; and the loss accompanying the shedding of leaves, etc., in the case of plants which live through more than one period of growth.

PLANT POSSESSING CHLOROPHYLL.

Income.	*Expenditure.*
I. *Matter.* Food; viz. Inorganic salts. Carbon dioxide. Water. Free oxygen.	1. *Matter.* *a. Accumulated.* Organic substance of tissues (protoplasm, cell-walls, etc.). Reserve materials (starch, sugar, fats, proteids, etc.). Unexcreted organic waste-products (tannins, alkaloids, acids, etc.). Mineral matter of ash. *b. Dissipated.* Carbon dioxide } in respiration. Water } Free oxygen (evolved by green parts in light). Incidental losses (reproduction, etc.)
II. *Energy.* Heat. Light (absorbed by chlorophyll).	II. *Energy.* *a. Accumulated.* Potential energy of the accumulated organic substance (see above). *b. Dissipated.* Heat. Light (in some cases). Movement (including growth). Potential energy (in connexion with the incidental losses of organic substance, as above).

In the case of plants which do not possess chlorophyll, the account must be altered thus:—

Income.	*Expenditure.*
I. *Matter.* Food; viz. Inorganic Salts. *Organic matter.* Water. Free oxygen (in most cases). II. *Energy.* Heat. *Potential energy of organic food.*	Same as in plant possessing chlorophyll, *except that no free oxygen is given off.*

CHAPTER III.

SPECIAL PHYSIOLOGY OF MOVEMENT.

§ 10. **Introductory.** The movements to be specially considered here are such as may be characterized as vital; that is, they are essentially manifestations of the life of the protoplasm. This statement is rendered necessary by the fact that movements do occur in plants which are dependent upon purely physical causes; instances of these are afforded by the rupture of pollen-sacs and other sporangia, the twisting and untwisting of awns (as in the fruits of Erodium, p. 612, and Stipa, p. 548), the bursting of fruits (as in the Balsam, *Impatiens Noli-me-tangere*, and the Squirting Cucumbers, such as Ecbalium, Momordica, and Elaterium). These movements may be due, in the simpler cases, either to expansion and contraction of hygroscopic cell-walls resulting from variations in the moisture of the air, or to the imbibition with water and the consequent swelling-up of mucilaginous substances in the cells; in the more complicated cases the movement depends upon tensions set up between different layers of tissue in consequence of unequal expansion.

The vital movements are either *spontaneous* or *induced.* In the former case they are the result of causes operating in the organism itself; in the latter, they are the result of causes acting upon the organism from without.

The following are the principal phenomena of movement exhibited by plants; the streaming movement of protoplasm (*cyclosis*); the expansion and contraction of contractile vacuoles; the locomotion of entire organisms; the movements of cellular members.

§ 11. **Automatism.** The spontaneous movements may be conveniently considered under the two heads of *movements of protoplasm*, and *movements of cellular members.*

A. Movements of Protoplasm. Under this head are included such spontaneous movements as can be directly observed in the protoplasm. The first to be noted is the streaming movement, which can be frequently observed either in naked protoplasm (*e.g.* plasmodia of Myxomycetes), or in the protoplasm of cœnocytes clothed by a cell-wall (*e.g.* hyphæ of Fungi), or in that of cells (*e.g.* leaf of Elodea and Vallisneria, internodal cells of Characeæ, root-hairs of *Trianea bogotensis*, hairs of the stamens of Tradescantia, etc.). The movement takes place in the more fluid portion of the protoplasm, and is made evident by the granules of various kinds which are carried along by the currrent. The direction of the movement varies somewhat according to circumstances: the current travels in one direction, and this simple longitudinal movement is all that can be observed in plasmodia and in hyphæ; but in cells, owing to their shortness, it can be observed to travel up one long side, across the end, and down the other side; and when the cytoplasm forms not merely a parietal layer, but has strands traversing the vacuole (*e.g.* Fig. 46 *D*), currents can be observed in these strands also.

The *contractile vacuoles* (see p. 102) are small, more or less nearly spherical, cavities which make their appearance in the protoplasm and then suddenly disappear. In their relatively slow expansion (diastole), they become filled with cell-sap, which is forced out on the sudden contraction (systole). They have been exclusively found in motile organisms, such as Volvox, Gonium, Eudorina, the plasmodia of Myxomycetes, the zoospores of many Algæ and of some Fungi.

In the second place the protoplasmic movements which involve locomotion have to be considered. The simplest case of this is the amœboid movement exhibited, among plants, by the zoospores of the Myxomycetes and of some Algæ, and by the naked masses of protoplasm which constitute the plasmodia of the Myxomycetes. There is here no specialised motile organ, but any part of the protoplasm may be protruded as a *pseudopodium* into which the remainder of the protoplasm gradually flows, and thus locomotion of the whole is effected.

The locomotory movements of most zoospores, of spermatozoids, and of entire organisms such as Volvox, Pandorina, etc., among Algæ, is effected by means of specialised motile organs, which are delicate protoplasmic filaments termed *cilia* (see p. 102); each cell may have one, two, four, or many cilia (see Figs. 168, 177, 181, etc.).

Locomotion is also exhibited by other Algæ, such as Diatoms, Oscillatorias, etc., as also by some Schizomycetes, but the mechanism is not fully understood.

B. Movements of Cellular Members. Instances of the movement of parts of plants consisting of one or more cells having a cell-wall, are afforded by all growing members, and by some specially modified mature members; the movements of the latter are termed *movements of variation*, those of the former, *movements of growth*.

These two kinds of movements can be readily distinguished from each other, inasmuch as the movements of variation are rapid and can be easily observed, whereas the movements of growth are slow and can only be followed by means of special apparatus.

a. Movements of Variation. The majority of the movements of variation are induced, a few only being spontaneous. Instances of spontaneous movement are afforded by the rising and falling of the lateral leaflets of the trifoliolate leaf of *Desmodium gyrans*, the Telegraph-plant; by the oscillation of the labellum of *Megaclinium falcatum*, an African Orchid; by the bending upwards and downwards of the gynostemium of *Stylidium* (*Candollea*) *adnatum* (see p. 692). It must, however, be pointed out that the power of spontaneous movement may be possessed by plants though they do not manifest it under ordinary circumstances. Thus the leaves of the Sensitive Plant (*Mimosa pudica*) move spontaneously in darkness, but they will not do so in the light. This is also true of various Leguminosæ and Oxalidaceæ.

b. Movements of Growth. Before entering upon a description of the movements of growth, a clear idea must be formed of what growth really is. By *growth* is meant change of external form, which is usually, though not necessarily, accompanied by increase in bulk; the change of form being rendered permanent by the deposition of new substance: it is a function of embryonic protoplasm (see p. 16).

The growth of the plant-body takes place to a greater or less extent in all three dimensions of space. For instance, when it takes place equally in all three dimensions, a spherical body is produced, as in Protococcus and Volvox. Occasionally it takes place especially in two dimensions, the result being a flattened body, such as a Fern-prothallus or an Ulva. More commonly, however, it takes place especially in one direction, so that the plant-body assumes an elongated form. An extreme case of this is afforded by Spirogyra and other filamentous Algæ. It is this *growth in length* which has been more especially studied physiologically, and in what follows, "growth" may be taken to mean "growth in length," unless there is some definite statement to the contrary.

The growth in length of the plant-body takes place at first throughout its whole extent; but at a later period it is limited, as a rule, to particular regions (see p. 16). In the growing portion of any member two regions may be distinguished: *the formative region*, which is the growing-point proper: and *the region of elongation* adjacent to it. In the formative region the construction of the new tissue from plastic substances takes place, as is specially manifested in the formation of cell-walls accompanying the cell-division going on in this region of a multicellular growing-point; but the amount of elongation is slight. In the region of elongation, the formative processes have ceased: in multicellular plants little or no cell-division takes place in this region; the cells are here fully formed, and they simply require to increase in bulk, to grow in fact, in order to attain the mature form. Beyond the region of elongation comes the portion of the member which has already ceased to grow. It must be clearly understood that each portion of the growing-point passes through these three phases. For instance, in a multicellular apical growing-point, each cell is produced in the formative region; and as in consequence of the continued formation of younger cells in front of it at the apex, it comes to lie at an increasing distance from the apex, it passes through the stage of growth, to become an adult tissue-element.

The movement of growth in length is altogether spontaneous. It may be generally described as the travelling of the organic apex in a line which is the continuation of the longitudinal axis of the growing member. Both the rate and the direction of growth are liable to variation, which may be either spontaneous or induced. The induced variations are discussed in § 12, p. 742.

Variations in the Rate of Growth. The rate of growth of a growing member, as also that of each of its constituent cells, is not uniform. When a member begins to grow, its rate of growth is at first slow; it then accelerates, until a maximum rapidity is attained; after which it diminishes until growth ceases altogether. This gradual rise and fall in the rate of growth, extending over the whole of one period of growth, is termed the *grand period of growth.*

This periodicity is manifested also in each cell of the growing region. A young cell grows but slowly; as it becomes older, and is gradually removed from the growing-point, its rate of growth increases up to a maximum; as it becomes still older and is still more remote, the rate of growth sinks, until finally the adult stage is reached, and growth ceases.

Careful observation of growing members has shown that, in addition to the spontaneous variation constituting the grand period of growth, small irregular variations are constantly taking place, which, since they are apparently spontaneous, are termed *irregular spontaneous variations.*

Another point which must be taken into account is the *energy of growth*; that is, the relative capacity of different members for growth in length. The differences in the energy of growth in growing members manifest themselves in differences either in the length of the grand period, or in the rate of growth; in other words, members may grow for a longer or shorter time, or they may grow more or less rapidly. In any case the result is that members attain different lengths. For instance, it is easy to observe that the lower internodes of most stems remain short; that those above them are longer; that those of a certain part of the stem are the longest; and that the upper ones again are short. In the same way the size of the leaves attached to these various parts of the stem increases from below to about the middle, and then diminishes.

Variations in the Direction of Growth. Although it is true, as stated above, that the result of growth is, generally speaking, that the apex of the growing member is moved onwards in a line which is the continuation of the axis of the growing organ; yet, during the actual process of growth, this relation of position is not maintained, because the rate of growth is at no time uniform throughout the transverse section of the region of elongation. Suppose a radial stem rising vertically from the soil; the longitudinal axis of the fully grown portion of this stem is vertical, but this is not true of the growing portion. If the apex be looked down upon from above it will be seen to travel in an orbit round the prolongation of the longitudinal axis of the fully grown portion, in the manner indicated by the following diagram.

FIG. 477.—The growing primary root of the Pea in two stages. *A* The root is marked by lines at equal distances. In *B* the differences in rapidity of growth are perceptible: the uppermost lines have not been separated; the root has ceased to grow here. The lowest likewise are still close together; at the growing-point elongation has not taken place. In the intermediate zone the elongation has been very great.

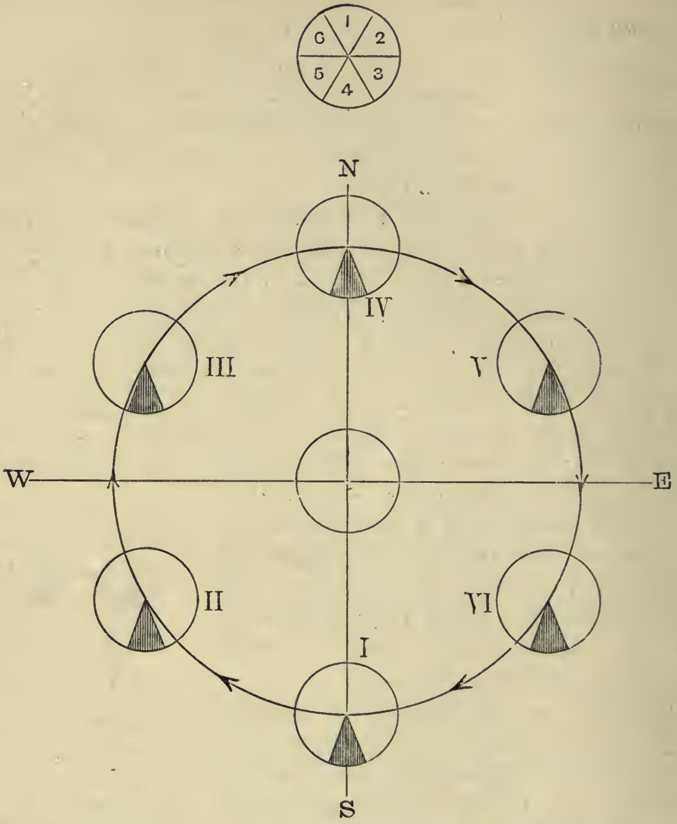

FIG. 478.—Diagram illustrating nutation of a cylindrical stem, as seen from above: N, S, W, E, indicate the points of the compass.

The small upper circle divided into segments represents an ideal transverse section of the nutating region: the larger circle below represents the orbit of nutation, and the small circles upon it represent different positions of the apex of the stem in its orbit; the shaded segment indicates always the position of one and the same side of the stem; the small circle in the centre of the orbit represents the position of the apex of the stem were it not nutating, but were it in a straight line with the older parts which have ceased to grow. Assuming, to begin with, that the rate of growth is uniform in all the segments of the elongating region, then the position of the apex will coincide with the small circle in the centre; but the growth is not uniform, being more active on one side than on the others, say in segment 1; then segment 4 will be the region of least active growth, and, as a consequence, the apex of the stem will be displaced southwards till it takes up a position *I* in the orbit; the wave of rapid growth then travels from segment 1 to segment 2, and the apex travels from position *I* to *II* in the orbit, and so on, until the apex has completed its orbit and returned to position *I*. It will be observed that the shaded segment always faces the same side (south) in all positions in the orbit; nutation is thus not accompanied by torsion, that is, by twisting of the member about its own axis. In this case the direction of nutation is that of the sun, or of the hands of a watch.

In this case, the stem being radially symmetrical, the orbit is approximately circular; but in cases in which the member tends to be bilaterally symmetrical, one diameter of the orbit becomes proportionally elongated, the orbit being then oval, or elliptic, until, finally, when the bilateral symmetry is strongly marked, the orbit becomes a straight line, the growing-point simply oscillating from side to side. Whilst the growing-point is travelling in its orbit, it is at the same time being raised upwards; so that it *describes a path* which is, according to the form of the orbit, a circular spiral, an elliptical spiral, or a zig-zag. These changes of position are, however, not permanent; for example, though the growing-point may be travelling upwards in a spiral, the fully-grown stem does not resemble a corkscrew, but is straight.

FIG. 479.—Illustration of the epinastic growth of the leaves of the Sunflower (*Helianthus annuus*). *A* represents the position of the leaves when the plant is exposed to light; *B* represents the position of the leaves when the plant has been kept in darkness for twenty-four hours. In *A* the leaves are expanded in consequence of the directive (diaheliotropic) action of the incident rays of light. In *B* the leaves, in the absence of light, had become recurved in virtue of their inherent epinastic growth.

These spontaneous changes in position of growing-points are designated generally by the term *Nutation.*

All growing members nutate in a more or less marked manner; but the most conspicuous instances are afforded by slender structures, such as tendrils, and the internodes of twining stems.

A peculiar form of nutation is commonly exhibited by dorsiventral members, such as leaves. In the early stages the one surface of the leaf grows much faster than the other, thus leading to certain peculiar forms of vernation and æstivation (see p. 60); in the later stages the other side grows the faster, and so the expansion of the leaf is brought about. When it is the ventral surface which is growing the faster, whether along the transverse or the longitudinal axis of the leaf, it is said to be a case of *epinasty* (Fig. 479); when the dorsal surface, it is said to be a case of *hyponasty.* A striking example is afforded by leaves having circinate vernation, as many Ferns, Drosera, etc.; this form of vernation is due to the growth of the leaf being at first longitudinally hyponastic. The convolute, involute, and conduplicate forms are all the result of transverse hyponastic growth in the early stages of development of the leaf, whereas the revolute form is the result of transverse epinastic growth.

§ 12. **Irritability** (*Induced Movements*). All parts of plants which can exhibit movement are also irritable; that is, they respond to the action of external agents either by a movement or by a change in the rate or the direction of their movement. The following are the principal causes, or *stimuli*, of movement, or change of movement:—

a. Mechanical; contact or pressure;
b. Variations of temperature;
c. Variations in the intensity of light;
d. Changes in the direction of incidence of the rays of light;
e. Changes of position with regard to the line of action of gravity (vertical);
f. Differences of degree of moisture in the surrounding medium.

a. Irritability to Mechanical Stimuli. This form of irritability is most strikingly manifested by motile mature members, and less markedly by certain growing members.

Irritability to contact is manifested by the following mature motile members: by the leaves of the sensitive plants (see p. 689), and by those of Dionæa and Drosera; by the stamens of Berberis, Mahonia, the Cynareæ, and the Cistaceæ; by the lobes of the stigma of Mimulus, Martynia, and Bignonia; and by the style of *Goldfussia anisophylla.*

The most familiar case is that of *Mimosa pudica*, the Sensitive Plant. The leaf of this plant is bipinnate, consisting of a primary petiole bearing at its free end four secondary petioles, upon which the leaflets or pinnæ are inserted (see Fig. 472). The primary petiole is articulated to the stem; each secondary petiole to the primary petiole; and each pinna to the secondary petiole, by a pulvinus. When stimulated, the pinnæ fold together forwards and upwards: the secondary petioles move sideways so as to come closer together and to lie almost parallel; and the primary petiole sinks downwards; the pulvini act as hinges upon which the various parts move.

It is only a few growing members which react perceptibly to mechanical stimulation; such are tendrils, the petioles of leaf-climbers (*e.g.* Tropæolum, *Lophospermum scandens*, Maurandia, *Solanum jasminoides*), the stem of at least one stem-climber, namely that of Cuscuta (Dodder), and roots. In these cases the contact must be of relatively long duration, becoming, in fact pressure.

It is still a question whether the internodes of all stem-climbers may not be in some degree sensitive to contact; but if so, they are sensitive only to long-continued contact.

The irritability of growing members to mechanical stimulation is, however, less marked than that of the mature motile members mentioned above. Even in the most sensitive growing members, such as tendrils, the resulting movement is comparatively slow. The movement induced in these members is that they tend to curve round the object with which they have come into contact. The result of this is that fresh portions of the member come into contact and are stimulated to curve, so that the member forms coils round the object, and thus becomes firmly attached to it. In the case of roots, when the growing-point is more or less injured by pressure or otherwise, a curvature is induced of such a kind that the injured side becomes convex, with the result that the growing-point, and consequently the direction of growth, is deflected from the obstacle or other cause of injury.

b. Irritability to Variations of Temperature. Movement, like the other functions (see p. 671), is affected by temperature, but this influence is not stimulating but *tonic*: it does not induce movement, but merely modifies the activity of movement (see p. 760). A sudden variation of temperature may, however, act as a stimulus and induce a movement. This kind of irritability has been detected in various leaves: for instance, a rise of temperature causes certain flowers (*e.g.* Tulip, Crocus) to open, and a fall of temperature causes them to close: similarly a fall of temperature causes the leaves of such plants as the Sensitive Plant and the Wood-Sorrel (*Oxalis Acetosella*) to fold up, whereas a rise of temperature causes them to expand (see Fig. 471).

c. *Irritability to Variations in the Intensity of Light* (*Paratonic Effect of Light;* p. 674). This is exhibited in a marked manner by the majority of motile members, more especially leaves. When, for instance, the intensity of the light is diminished, the perianth-leaves of many flowers and the foliage-leaves and cotyledons of many plants perform movements which are termed *nyctitropic* or *sleep-movements* (see p. 689). Thus, the flowers close; and the foliage-leaves change their position in various ways, assuming what is known as the nocturnal position, so that they no longer present the surface, but the margin of the blade to the sky. Conversely, when flowers or leaves which have assumed the nocturnal position are exposed to light, or to brighter light than before, they resume their normal expanded (diurnal) position.

Another remarkable manifestation of this irritability is that movements of variation in some cases, and movements of growth in most cases, are retarded or arrested by exposure to light of a sufficient intensity.

In illustration of the effect of light upon movements of variation, it may be stated that certain members, such as the leaves of the Sensitive Plant, which perform spontaneous movements of variation, are unable to do so when exposed to bright light: under this condition the leaves become fixed, as it were, in the diurnal position. This is not, however, the case with all mature motile members: for instance, the movement of the lateral leaflets of the Telegraph-plant (*Desmodium gyrans*) continues even in bright sunlight.

The paratonic action of light on movements of growth is strikingly exhibited in various ways. It is well demonstrated by *etiolated* plants (see p. 674), that is, by plants which have been kept in darkness for some considerable time. A characteristic feature of etiolated shoots is the excessive length of their internodes, as compared with those of a shoot which has been growing for the same period exposed to the normal alternation of day and night. This excessive elongation in darkness—which occurs as a rule in all radial and isobilateral members which usually grow exposed to light—is the result of the absence of the retarding paratonic action of light.

The exceptions to this rule are the shoots of stem-climbers (Hop, etc.). The stems of these plants have, under ordinary conditions, very long internodes; they seem to grow to the utmost even although they are exposed to light, and they do not grow to any greater length in darkness. On account of this peculiarity they have been termed "normally etiolated shoots."

The effect of the paratonic action of light can also be estimated by direct measurement of the growing member. As the result of a great number of comparative measurements, it has been found, in regard to members of all kinds, that the rate of growth is more rapid in darkness than in light.

An interesting demonstration of the relation of the rate of growth to light, is afforded by the observation of the growth of any member at given intervals—every hour, or every two or three hours—during an entire day of twenty-four hours. By this means it has been ascertained that a growing member exhibits a regular *daily periodicity* in the variations in its rate of growth, which has a direct relation to the alternation of day and night.

A general inspection of the tracings in Fig. 480 shows that the rate of growth increases in darkness, and diminishes in the light. This is more apparent in the 3-hour than in the 1-hour tracing, for the latter is complicated by the registration of the spontaneous variations in the rate of growth (see p. 739), whereas the former is not, owing to the longer interval between the measurements.

It will be further noticed that the effect of a change from darkness to light, or from light to darkness, is not manifested at once; but that after such a change, the rate of growth goes on, for a time, as it did before, until gradually it alters. In fact, a growing member, though kept in continuous darkness, will exhibit a more or less well-marked periodicity for several days. This is a good instance of the general slowness of reaction which characterises growing members.

But it must be borne in mind that variations of temperature also affect the rate of growth. Hence, since the alternation of day and night is accompanied by changes of temperature, the forms of the tracings in the figure are not solely due to the influence of light, but also to some extent to that of temperature. Speaking generally, it may be said that, as the intensity of the light diminishes towards evening, the temperature falls. The former condition tends to accelerate growth, but the latter to retard it. The actual rate of growth is the resultant of the acceleration due to diminished light, and of the retardation due to a falling temperature. Similarly, in the morning, the increasing intensity of the light tends to retard growth, whereas the rising temperature tends to accelerate it. The actual rate of growth is the resultant of the retardation due to increased intensity of light, and of the acceleration due to a rising temperature.

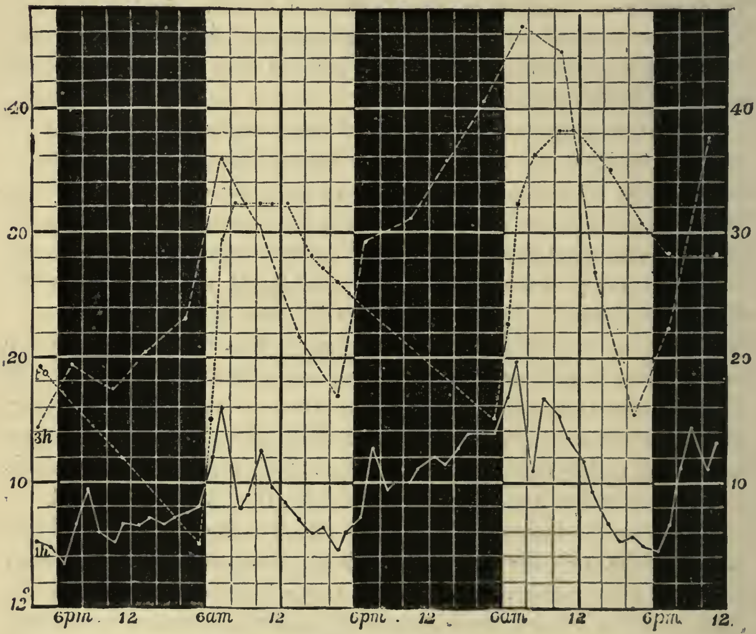

Fig. 480.—(After Sachs). Illustrating the daily periodicity of growth in length.

In Fig. 480 there is given a graphic representation of two complete *daily periods* of growth as observed in a Dahlia-stem. The abscissæ of the base-line represent periods of two hours, and the divisions of the ordinates represent units of growth in length. The tracing marked $1h$ is the result of hourly measurements of the growing stem; the tracing marked $3h$ is the result of measurements made every three hours. The variations of temperature have been also taken into account, and are represented by the tracing marked $t°$: the base-line represents 12° R., and five of the divisions of the ordinates represent 1° R.: it will be seen that the temperature varied between about 12.5° R. and 15.8° R. The shaded spaces represent periods of darkness.

The paratonic action of light varies with its intensity: the more intense the light the more marked the paratonic action. Exposure to very intense light may entirely arrest growth for the time being.

It has been found that the different rays of the spectrum are not equally active; the paratonic effect of the more highly refrangible rays (violet, indigo, blue) is far greater than that of the rays of lower refrangibility (see Fig. 481).

d. Irritability to the Direction of Incidence of the rays of Light (Heliotropism). This kind of irritability is extremely common, and generally manifests itself in the most striking manner. The most active rays of light are those of high refrangibility (violet, indigo, blue).

A remarkable example of this is afforded by the zoospores of various plants (*e.g.* Ulothrix, Hæmatococcus, Botrydium, etc.).

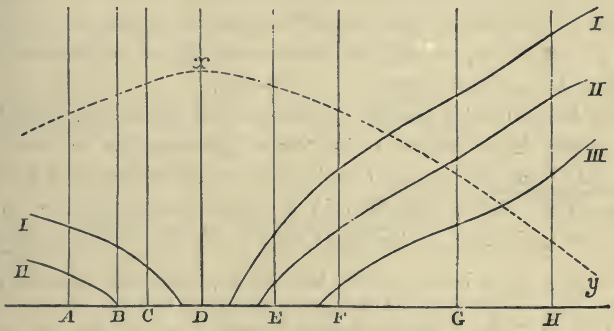

Fig. 481.—(After Wiesner). Curve illustrating the relative heliotropic effect of rays of different refrangibility. The letters *A—H* in the base-line indicate the position of the more important lines in the solar spectrum. The curves *I, II, III* represent the degree of curvature, under the influence of the different rays, presented by the Vetch, the Cress, and the Willow respectively. The curve *xy* represents the relative effect of the different rays in retarding growth; it is greatest at *y*, and least at *x*.

When light falls obliquely upon them, these zoospores arrange themselves in the water so that their long axes are parallel to the direction of incidence of the rays; this phenomenon is termed *Phototaxis.* Moreover, the direction of their movement is also determined by the direction of incidence of the light. They move in the line of incidence, but they may move either towards or away from the source of light; the direction depending partly on the intensity of the light, and partly on the degree of irritability of the zoospore. When a zoospore moves towards a source of light, it is said to be *positively phototactic*; when away from it, *negatively phototactic.*

Another important case is the change of position of the chlorophyll-corpuscles in the cells (see p. 686).

Motile cellular members, whether mature or growing, are, as a rule, sensitive to the directive influence of the incident rays of light. Among mature motile members, foliage-leaves are those which most markedly respond to the directive or heliotropic influence of light; among growing members, it is more especially stems and leaves which are sensitive, but roots have in many cases been found to be so. All these irritable members take up a definite position, the *light-position* (p. 688), with reference to the direction of incidence of the rays of light. Members capable of performing movements of variation can, if necessary, change their light-position, whereas the light-position of other members can only be changed so long as they are growing.

The particular position which the member assumes under the heliotropic influence of light, depends upon its organisation. Three classes of members, namely the dorsiventral, the isobilateral, and the radial, have therefore to be considered.

It may be generally stated of dorsiventral members, that, for a certain mean intensity of light, their light-position is such that the morphologically upper (ventral) surface is directed towards the source of light, and lies in a plane perpendicular to the direction of incidence of the rays: that is, they are *diaheliotropic*.

It must, however, be borne in mind that the position of dorsiventral members with regard to light may not, in nature, always be found to be exactly that described above, because other directive influences are in operation which interfere with the effect of light. When, by appropriate arrangements, the effect of the other influences is removed, and light alone is acting, the truth of the above statement will be demonstrated.

The case of motile foliage-leaves may be taken first in illustration, such as those of the Sensitive Plant, Robinia, Scarlet Runner, etc. When these leaves are exposed to light of sufficient intensity to cause them to assume the diurnal position (see p. 689), their upper (ventral) surfaces are at right angles to the direction of incidence of the rays. If, on the one hand, the light to which they are exposed becomes less intense than this, they will manifest no sensibility to its direction of incidence, but will merely assume the nocturnal position. If, on the other hand, the light becomes more intense, then the leaves will alter their position so that the blades will present their edge, instead of their ventral surface, to the incident rays (paraheliotropism, see p. 689).

In the case of foliage-leaves and other dorsiventral members which cannot execute movements of variation, the light-position is assumed in the course of development, and is fixed. Since it cannot be altered in relation to variations in the intensity of the incident rays, the position assumed is determined by the most frequent direction of incidence of the rays of suitable intensity. For instance, the fixed light-position of the foliage-leaves of plants growing free in the open, is usually not such that the ventral surface is horizontal, facing the zenith; but such that it is directed towards that quarter of the sky from which, not the brightest sunlight, but the brightest diffuse daylight, falls perpendicularly upon it. In fact, it is not unusual to find that the fixed light-position of leaves, when the light is of high average intensity, is such that the surfaces are vertical, so that the margin is presented to the zenith. Under these circumstances both surfaces are equally exposed to light, and the structure of the leaf becomes more or less isobilateral (see pp. 164, 686).

A most remarkable instance of a fixed light-position with vertical surfaces, is afforded by the so called "Compass-plants," *Silphium laciniatum*, and *Lactuca Scariola*. The surfaces of the leaves of these plants are not only vertical when fully exposed to bright light, but they place themselves in a vertical plane which more or less nearly coincides with the meridian of the locality, the surfaces of the leaves facing east and west. It is this relation of the fixed light-position of the leaves to the points of the compass which suggested the name "Compass-plants."

The fact that the ultimate position of dorsiventral leaves is mainly determined by light, is demonstrated by removing them—whilst still growing, and therefore capable of a change of position—from its influence. In darkness these leaves take up an altogether different position (see Fig. 479), becoming curved in various ways; when again exposed to light they resume their previous diaheliotropic position.

With reference now to radial members, it may be generally stated that the essential feature of their response to the directive influence of light is that they tend to place their long axes in the direction of incidence of the brightest light falling upon them. Whereas in the case of dorsiventral members the important point is the *relation of the morphologically upper surface* to the direction of the incident rays; in the case of radial members the important point is the *relation of the long axis* to the direction of the incident rays.

An exact coincidence between the direction of the long axis of the member and that of the incident rays is, however, not always attained in nature, on account of the antagonistic action of other directive influences. This point is more fully discussed on p. 757.

It must be mentioned that, inasmuch as there are no radial members which are both heliotropically irritable and capable of performing movements of variation, all that is here said refers to growing radial members.

In illustration, the case of a radial member which has been grown in the dark may be taken, and it may be assumed to be vertical. Light is allowed to fall upon it from one side; the effect is a gradual curvature of the member, as it continues to grow, so that its long axis comes to coincide more or less nearly with the direction of the incident rays.

But the curvature may be in one of two directions; it may be either such that the apex of the member comes to point towards the source of light, or such that it points in the opposite direction. When the former is the case the member is said to be *positively heliotropic*; when the latter, it is said to be *negatively heliotropic*.

The nature of the curvature, whether positive or negative, depends upon the specific irritability of the member. Thus, generally speaking, primary shoots, including such forms as the stems of Chara and Nitella, the peduncles of flowers, the stipes of the larger Fungi, and the gonidiophores of Moulds, as also radial leaves such as those of the Onion, are positively heliotropic. Negative heliotropism has been observed in many roots, especially aerial roots, and in the root-hairs of Marchantia. With regard to shoots, the hypocotyl of Viscum, the Mistletoe, is negatively heliotropic.

Although the relation between the external symmetry of the member and its heliotropic irritability is generally that indicated above, yet there are exceptions: all dorsiventral members are diaheliotropic; but not all radial members are positively or negatively heliotropic, for some of them are diaheliotropic. It seems that continual exposure to intense light falling on one side induces at least physiological dorsiventrality in some radial members (*e.g.* shoots of Ivy and Tropæolum).

It is frequently stated that exposure to intense light causes a *reversal* of heliotropic properties in radial members; for instance, that a shoot which is positively heliotropic in moderately intense light becomes negatively heliotropic in very intense light. The true explanation of such cases is probably this, that under the influence of intense unilateral illumination, the radial organ becomes physiologically dorsiventral; it is then diaheliotropic (*not* negatively heliotropic) in place of being positively heliotropic, and any curvature which it may present is due to epinasty or hyponasty.

The flattened, typically isobilateral, leaves of various Monocotyledons, such as those of Iris, appear to be positively heliotropic.

e. Irritability to the Directive Influence of Gravity (*Geotropism*).

The effects of the stimulating directive action of gravity must be clearly distinguished from those which are due to the mere weight of the parts. It is only the former which are referred to by the term *geotropism.* The geotropic curvatures are effected with considerable force, and will take place even against considerable resistance; for instance, it has been observed that the primary roots of seedlings will curve downward into mercury.

Geotropic irritability is manifested by various members, such as stems, leaves, and roots. The phenomena of geotropism in the three categories of members, the dorsiventral, the radial, and the isobilateral, will now be studied.

With regard to dorsiventral members, it appears that many leaves, both growing and motile, lateral shoots of Conifers and of many dicotyledonous shrubs, runners, etc., which are dorsiventral, take up such a position, when acted upon solely by gravity, that their longitudinal axis is horizontal—that is, at right angles to the line of action of gravity, the vertical—and that their morphologically superior surface is directed upwards. If these members are moved out of this position so that their long axis is not horizontal, they curve until it is so; or if they be so moved that the normally upper surface faces downwards, they twist until it faces upwards. These members behave in respect to the line of action of gravity just as they do to the direction of the incident rays of light. They are *diageotropic*, just as they are diaheliotropic.

It is a familiar fact that at all points of the earth's surface typical radial members, such as primary shoots and roots, grow with their long axis vertical, but with this difference, that the direction of growth of the primary shoots is away from the centre of the earth, whereas that of the primary roots is towards the centre of the earth. It can be readily demonstrated (by Knight's machine, Fig. 483) that this vertical direction of growth is due to the force of gravity, that it is, in fact, a phenomenon of geotropism. But the effect produced is precisely opposite in the two cases; primary shoots grow in a direction opposed to that of the action of gravity, they are *negatively geotropic*; primary roots grow in the same direction as that of the action of gravity, they are *positively geotropic*. If these members be moved out of their normal position, they will return to it by performing geotropic curvature.

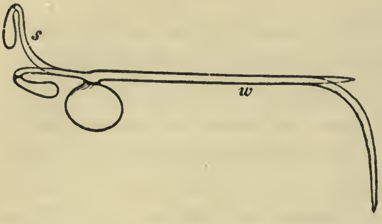

FIG. 482.—Geotropic curvature of a Pea-seedling placed horizontally. The thicker outline indicates the original positions of the primary shoot and root; the shoot *s* has curved upwards in the course of its growth, the root *w* has curved downwards. The bud at the apex of the shoot is nutating.

The principle of Knight's machine is to expose growing plants to the action of centrifugal force, either alone (Fig. 483 *B*) or together with gravity (*A*). The object of it is to demonstrate that gravity is the directive force which determines the relative directions of growth of shoots and roots; the line of reasoning being, that if the direction of growth of roots and shoots can be affected by a known physical force, such as the centrifugal force of a rapidly rotating wheel, in a manner analogous to that observable in nature, it may be concluded that the natural direction of growth of these members is the result of the action of a physical force, and this force is doubtless that of gravity. In Fig. *A*, the seedlings have been grown on a rapidly rotating horizontal wheel, and exposed consequently to the action both of gravity and of centrifugal force: the result is, that the primary roots and shoots still grow in diametrically opposite directions, but the line of growth is not vertical, as in nature, but oblique; hence it follows that the direction of growth of both root and shoot has been affected by the centrifugal force. In *B*, the seedlings have been grown on a rapidly rotating vertical wheel: in consequence of the continuous change in position with regard to the vertical, it is obvious that, in this experiment, the directive action of gravity is eliminated, for all parts of the seedlings are acted upon by gravity for successive equal times in opposite directions: the only force in action is the centrifugal force, with the result that the primary roots have grown towards the centre of the wheel, in a direction contrary to that of the line of action of the centrifugal force, whilst the primary shoots have grown outwards, away from the centre of the wheel, in the same direction as the action of the centrifugal force. It is clear from these facts (1) that a purely physical force can determine the direction of growth of roots and shoots: (2) that the physical force employed (centrifugal force) affects primary roots and shoots in a precisely contrary manner: and it may be concluded that since the phenomena produced by the action of centrifugal force in these experiments are quite analogous to those observable in nature, the cause of the natural phenomena is also a purely physical force, and the force of gravity is the one which meets all the necessary conditions.

Another mode of experimental proof is by means of a machine termed a *clinostat*. This machine differs from Knight's machine in that the rotation of the plant is very slow, so that no centrifugal force is set up. The principle of it is that, by slowly rotating a plant by means of a vertical wheel either (as in Fig. 483 *B*) with the long axis of the plant in the plane of the wheel, or with the

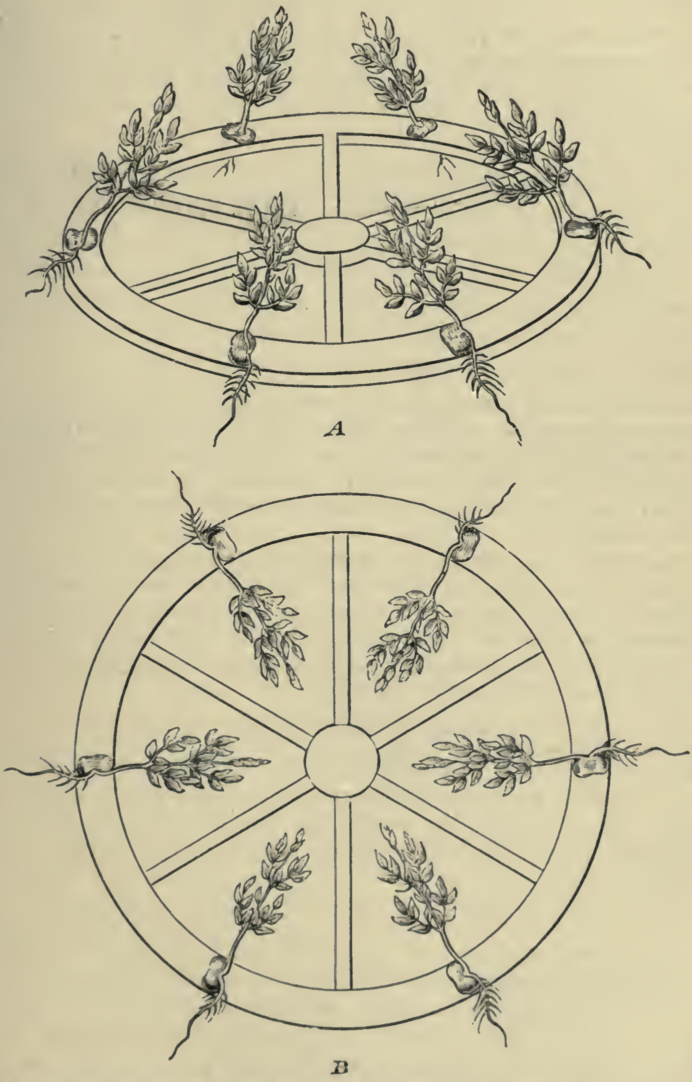

FIG. 483 (after Knight).—Diagrams illustrating experiments with Knight's machine. *A* Wheel rotating horizontally on a vertical axis; *B*, wheel rotating vertically on a horizontal axis.

long axis of the plant perpendicular to the plane of the wheel, each part is exposed for successive equal times to the action of gravity in precisely opposite directions, so that the directive action of gravity neutralises itself. The result is that a stem or root with its long axis horizontal remains perfectly straight when rotated on the clinostat, provided that other disturbing influences (light, etc.) are excluded; and the fact that the empirical results given by the machine exactly correspond to what would be theoretically anticipated on the hypothesis that gravity is the active directive force in geotropic curvature, is strong confirmatory evidence of the conclusions to be drawn from experiments with Knight's machine.

The geotropic influence of gravity is greatest when the radial member is in a horizontal position; that is, the curvature into the normal position then takes place with the greatest rapidity. But the visible effect is the more marked, the further the member is removed from its normal position; for instance, when a primary shoot is turned upside down, a curvature of 180° has to be performed in order that the apex may again point upwards.

In addition to the primary shoots of seedlings, the following radial members are negatively geotropic; the stipes of Mushrooms, the gonidiophores of Moulds, the stems of Characeæ, the stalks of the receptacles of Liverworts, the peduncles of many flowers, the setæ of Mosses, etc. Also isobilateral leaves, such as those of Iris; when placed horizontally in darkness, whether flat or edgeways, they curve upwards.

In addition to the primary roots of seedlings, the following radial members are positively geotropic; the hyphæ of Fungi which penetrate into the substratum, the root-like filaments of Vaucheria, and other Algæ, the rhizoids of Muscineæ, the rhizomes of *Yucca filamentosa* and of *Cordyline rubra*, etc.

An instance of the absence of geotropic irritability in a growing member is afforded by the hypocotyl of the Mistletoe.

The degree of geotropic irritability is not the same in all radial members. It may be generally stated that the lateral branches both of shoots and roots are less irritable than primary shoots and roots. For instance, the secondary branches of roots grow, not vertically downwards, but obliquely outwards and downwards, in the soil.

All radial members are not, however, either positively or negatively geotropic; some, such as the rhizomes of *Heliocharis palustris*, *Sparganium ramosum*, and *Scirpus maritimus*, are diageotropic.

It has been observed in some cases that the nature of the geotropic irritability of a member may change in the course of its development. For instance, the peduncle of the Poppy is positively geotropic whilst the flower is in the bud, but negatively geotropic during flowering and fruiting. Again, the flowers of the Daffodil are negatively geotropic when in the bud, but they become diageotropic as they open.

f. Irritability to Differences in the degree of Moisture in the surrounding Medium (Hydrotropism).

Irritability of this kind is especially characteristic of earth-roots which possess it in a high degree. It can be readily demonstrated by a well-known experiment. Peas or Beans are made to germinate in a sieve full of damp sawdust, the sieve being suspended in a slanting position. The primary roots grow downwards through the sawdust, and escape into the air (which is kept moist). At first they grow vertically downwards in consequence of their positive geotropism, but they soon curve upwards towards the moist surface. They do this in virtue of their hydrotropic irritability, and it is clear that they are positively hydrotropic.

g. Irritability of other kinds. It has been ascertained by experiment that members of various kinds may be stimulated to curvature by other causes, such as differences of temperature on the two sides, galvanic currents, the flowing of currents of water, and by the presentation of various chemical substances; but these various phenomena are not of such immediate importance to the well-being of the plant as those which have been described above in detail.

The stimulating action of certain chemical substances (*chemiotaxis*) is, however, of some importance in connexion with the reproductive processes. It had been frequently observed that the motile male cells (spermatozoids) of plants possessing them appeared to be attracted to the female organ, fertilisation being thus ensured, but the cause of this has only recently been ascertained, and only in certain cases. It appears that the female organ, when it is fit for fertilisation, excretes into the surrounding water a substance which attracts the male cells. In Ferns and Selaginella this substance is a compound of malic acid; in Mosses it is cane-sugar.

§ 13. **Localisation of Irritability.** Among members which perform movements of variation, there are many instances of well-defined localisation of irritability. Thus, in the Sensitive Plant, no movement ensues when the upper side of the pulvinus of the primary petiole is touched, but only when the sensitive hairs on the under side of the pulvinus are touched; and, in the leaflets, it is the upper side of the pulvinus which is sensitive. In Drosera, the irritability of the tentacles is localised in the terminal gland. In Dionæa, movement only ensues when the irritable hairs on the upper surface of the leaf are touched.

Among growing organs, tendrils offer well-marked localisation of irritability. In most tendrils the lower or basal part is either not at all sensitive, or is sensitive only to prolonged contact. Most tendrils have their tips slightly hooked, and their irritability is localised in the concavity of this curvature. The tendrils of *Cobœa scandens* and of *Cissus discolor* are irritable on all sides; in those of Mutisia the inferior and lateral surfaces are irritable, but not the superior. The irritability of the root to the pressure of obstacles (see pp. 683, 743) is localised in the tip.

The foregoing examples sufficiently prove the localisation of irritability to mechanical stimulation: and the question arises whether or not irritability to other stimuli is also localised. It has been ascertained that this is the case, in connexion with heliotropism and geotropism, at least in certain plants. Thus, the heliotropic irritability (*i.e.* sensitiveness to the directive influence of light) of the cotyledons of certain Grasses, though not absolutely confined to the tip, has been found to reside especially in that part, and the same is the case with the primary shoot of many dicotyledonous seedlings and with young shoots of various plants. The geotropic irritability of roots also resides in the tip, and this appears to be also true of other members.

§ 14. **Transmission of Stimuli.** The most striking instances of this are offered by motile leaves, such as those of the Sensitive plant and of Drosera. If the terminal pair of leaflets of a pinna of the leaf of the Sensitive Plant be irritated, not only will they fold up, but each of the other pairs of leaflets of the same pinna will fold up in succession; if the stimulus is sufficiently strong, its effect may extend to other pinnæ causing their leaflets to fold up, or to the secondary petioles causing them to converge, or even to the main petiole which then sinks downward (see Fig. 472). Stimulation of one leaf, if sufficiently powerful, will cause movement in another. In the case of Drosera, stimulation of the central tentacles of a leaf causes the inflexion of the marginal tentacles.

In so far as heliotropic and geotropic irritability is localised in the tips of growing members, these must also afford instances of transmission of stimuli. The stimulus acts upon the irritable tip, and the impulse is transmitted to the region in which the curvature takes place.

The means by which stimuli are transmitted is a matter which is still under discussion; but it appears that the means of transmission is not the same in all cases. Whilst in some, such as tendrils and the leaves of Drosera, the stimulus is probably transmitted by means of the delicate protoplasmic filaments which connect the protoplasm of adjacent cells (see p. 91); in others, for instance *Mimosa pudica*, the stimulus is transmitted as a disturbance of the hydrostatic equilibrium of the cells: it would, in fact, appear that whilst the former means of transmission suffices for a short distance, the latter is necessary when the distance to be traversed is considerable. In *Mimosa pudica* there appears to be a special tissue along which the stimulus is conducted: it belongs to the bast, and consists of large elongated cells with pitted cellulose walls.

The Latent Period. It has been observed, more especially with regard to the heliotropic and other curvatures of radial growing organs, that the curvature does not become apparent for some considerable time after the stimulus has begun to act. This interval is the *Latent Period.* For instance, it has been ascertained that the primary shoots of Bean-seedlings do not begin to curve heliotropically for two hours after an exposure of one hour to unilateral illumination.

When, however, the stimulus to curvature has acted for a sufficient time, the curvature will eventually take place even though the stimulus has ceased to act: the conditions of curvature have been induced, that is, even before the curvature can be observed.

In explanation, it may be suggested that, in growing members, the stimulus is conveyed but slowly from the seat of irritability to the seat of curvature; and it is obvious that the curvature of a growing cellular member is a process which, on mechanical grounds in relation with the rate of growth, cannot be effected rapidly.

§ 15. **Combined Effects of different Stimuli.** Inasmuch as it is commonly the case that the motile members, whether growing or mature, are irritable to stimuli of various kinds, it is clear that the assumption by them of any particular position is the resultant effect of the stimuli which may be acting simultaneously. The phenomena in question are strikingly manifested by growing members, and it is to these that the following account especially refers.

According to the position assumed in the course of their growth under the influence of various external directive influences, plant-members may be conveniently classified into those which have their long axis vertical, and those which have their long axis oblique or horizontal, the former are distinguished as *orthotropic*, the latter as *plagiotropic*. Most radial and isobilateral members are orthotropic; all dorsiventral, and some radial members are plagiotropic. For instance, radial primary shoots and roots are orthotropic; all dorsiventral leaves, etc., are plagiotropic; lateral branches of shoots and roots, even though radial, are plagiotropic.

The directive influences which mainly determine the direction of growth of radial primary shoots are gravity and the direction of the incident rays of light, and the shoots themselves are negatively geotropic and positively heliotropic. If only the conditions are such that each side of the shoot receives an equal amount of light, as when the plant grows quite in the open, no heliotropic curvature takes place, and the shoot grows erect. But when one side of the plant is shaded, as when it grows by the side of a hedge, the shoot in most cases curves heliotropically out of the vertical. This curvature is the resultant effect of the negative geotropism of the shoot which tends to keep it straight, and its positive heliotropism which tends to make it curve more than it actually does. Unilateral illumination usually causes some degree of curvature in shoots, because, as a rule, their heliotropic irritability is higher than their geotropic irritability. Exceptions to this rule have been found in the inflorescences of Verbascum and Dipsacus, which remain erect even when one side is shaded.

Similarly, the influences which ordinarily determine the direction of growth of radial primary roots, are gravity and the distribution of moisture in the soil. If the soil is uniformly moist, the root grows vertically downwards under the influence of gravity; but if the soil is not uniformly moist, the root will curve out of the vertical towards the moister area, because its hydrotropic is greater than its geotropic irritability.

The conditions which determine the plagiotropic position of most radial lateral branches of shoots are these: they are negatively geotropic, and they are diaheliotropic, at least in intense light. In darkness they grow erect, in virtue of their negative geotropism. Some radial subterranean rhizomes are, however, diageotropic (see p. 754). The oblique growth of lateral roots is simply due to their feeble geotropic irritability.

The conditions which determine the plagiotropic position of dorsiventral members are these: they are both diageotropic and diaheliotropic. But inasmuch as their heliotropic is higher than their geotropic irritability, their ultimate position is that in which the incident rays of appropriate intensity fall nearly or exactly at right angles upon the upper surface.

It will be observed that, as a rule, in growing members which are heliotropically irritable, this irritability is higher than any other; consequently the ultimate position assumed by the member is mainly determined by the direction of the incident rays of light, and it is termed, therefore, a *light-position* (see p. 748), although other directive influences may have contributed to its assumption.

The most remarkable case of combined effects is afforded by the growth of twining stems. A twining stem, at its first development, is straight, but after it has come to consist of two or three internodes its apex hangs over to one side, for the stem is not sufficiently rigid to support its own weight. It then exhibits circumnutation in a marked manner. If once it comes into contact with a more or less vertical support of appropriate thickness, it twines round it.

The analysis of the phenomenon of twining is still a matter of discussion. The main facts are the following. Twining stems are strongly negatively geotropic; this is proved by the fact that they will not twine round very oblique or horizontal supports. Again, contact with a support interferes mechanically with the circumnutation of the stem, and causes it to take place in an orbit of which the support is the axis. Finally, a twining stem usually undergoes torsion, that is, a twisting about its own axis, and this has been suggested as an essential factor in the process of twining; but there is not evidence to support this suggestion.

The commonly accepted explanation of twining is that it is due to the negative geotropism of the stem, combined with its circumnutation modified by contact with the support; but it is doubtful if this explanation is adequate. It has been suggested, with some show of reason, that twining stems are irritable, like tendrils, though in a less degree, to continuous contact with a support. It is admitted that the stem of the Dodder (see pp. 685, 743) is thus irritable. If this be so, then the irritability of twining stems is the most important factor in the process.

In order to investigate independently the degree and the kind of geotropic and heliotropic irritability of a member, it is necessary to be able to exclude the directive influence of light and of gravity. The influence of light can be easily elimated by performing the experiments in darkness, or by rotating the plant so that each part of the member under observation is exposed for equal lengths of time to rays of light falling upon it in all directions, so that the heliotropic effect is the same on all sides, and no curvature is produced. The influence of gravity can likewise be eliminated by slowly rotating the plant, so that each side of the organ is placed for equal times successively in all possible positions with respect to the vertical; the geotropic effect is therefore the same on all sides, and no curvature is produced. The instrument used for this purpose is the clinostat (see p. 752).

§ 16. **Conditions of Movement.** Inasmuch as the movements under consideration are vital, they can only take place when the external conditions are favourable to the life of the plant. The following conditions are essential; a moderate temperature, extremes of heat and cold arrest movement; a supply of water, all movements are arrested by drought; a supply of free oxygen, in the case of aerobiotic plants (p. 722); and, in some cases, exposure to light of a certain intensity.

The importance of exposure to light as a condition of movement requires special consideration. It has been ascertained to be essential to movements of the most different kind. For instance, a Bacterium (*Bacterium photometricum*) has been found to be motile only when exposed to light. Again, various movements of variation, such as those of the foliage-leaves of Mimosa, etc., do not take place unless the plant either is, or recently has been, exposed to light. But the most important case is the arrest of growth of dorsiventral members when kept in darkness. For example, if a potato-tuber sprouts in a dark chamber, the produced shoots have excessively elongated internodes (see p. 674), but very small leaves; the growth of the leaves is arrested in darkness. On the other hand, intense light retards movement (*e.g.* its action on growth) or altogether arrests it (*e.g.* arrest of spontaneous movement of the leaves of the Sensitive Plant).

What is exactly the influence of light in promoting movement is not understood, but it is termed the *phototonic* influence (p. 674): it induces, that is, a particular condition, the condition of *phototonus*, in the protoplasm, without which movement is impossible. It appears that the rays of low refrangibility (red-yellow) are most favourable for the phototonic condition.

Irritability also depends upon the above essential conditions: in fact, induced movements are more rapidly arrested by unfavourable conditions than are spontaneous movements. For instance, when a Sensitive Plant is kept in continuous darkness, the leaves first lose their power of responding to stimuli, and later their spontaneous movements cease.

Irritability may also be abolished by special means. For instance, exposure to the vapour of chloroform or ether destroys the irritability of the leaves of the Sensitive Plant. Again, it may be abolished by repeated stimulation, the interval between the stimulations being very short. This has been observed in the case of the leaves of the Sensitive Plant and of Dionæa.

§ 17. **Mechanism of the Movements.** The ultimate factor in the mechanism of the vital movements of plants, whether spontaneous or induced, is the *motility* of the protoplasm (see p. 670).

Though the intimate mechanism of the motility of protoplasm is not fully understood, yet a consideration of the mechanism of the movements described above will be instructive. With regard to the streaming movement of the protoplasm, it is probably due to wave-like contractions and expansions of the protoplasm. The mechanism of the movements of the contractile vacuoles appears to be this: the systole of the vacuole is due to the sudden active contraction of the protoplasm, the contained liquid being expelled; the diastole, to the active but gradual expansion of the protoplasm, the cavity of the vacuole, as it enlarges, being filled with liquid. The protrusion and retraction of pseudopodia in amœboid movement may be accounted for in the same way; the protrusion is probably analogous to the diastole of the contractile vacuole, the retraction to the systole. A similar explanation may be offered of ciliary movement.

The movements of cellular members take place in a definite region, which may be distinguished as the motile region; this is, in growing members, the region of elongation (see p. 738); and, in mature members, is a more or less well-marked region of motile tissue which may constitute a distinct motile organ (*e.g.* pulvinus of a motile leaf). The movements depend essentially upon variations in bulk of the cells, and these, in turn, upon variations in turgidity (see p. 668). It is clear that if the turgidity, that is the hydrostatic pressure of the cell-contents, increases, the cell will expand provided that the wall be extensible; and conversely, that if the turgidity diminishes, the cell will shrink, provided the wall be elastic. Movement can only take place when the cell-walls possess these physical properties: hence, the pulvinus of mature motile leaves consists mainly of parenchymatous cells with unlignified walls, the lignified tissue being reduced as much as possible: similarly, in the elongating region of growing-members the cell-walls are thin and unlignified. But whilst the movements of variation (p. 737) are the result of a sudden loss of turgidity, which is either spontaneous or the effect of stimulation, the movement of growth depends upon the maintenance of turgidity, and the variations in the rate of growth (see p. 738) are the expression of variations in the degree of turgidity.

Brief allusion may here be made to the controversy as to the mechanics of growth of the cell-wall. The two conflicting theories are (1) the theory of *intussusception*, according to which the growth of the cell-wall is due to the intercalation of new particles (micellæ) of solid substance between the already existing particles of the wall; and (2) the theory of *apposition*, according to which the growth of the cell-wall is due to the repeated deposition of layers of substance on the internal surface of the original wall. Neither of these theories gives a completely satisfactory explanation of all the phenomena of growth of the cell-wall, nor are they mutually exclusive. It seems that the growth in surface of the cell-wall can be most satisfactorily explained on the intussusception-theory, and the growth in thickness on the apposition-theory. Both theories, as generally stated, seem to involve the assumption that the growth in surface of the cell-wall is dependent upon the turgidity of the cell: but this assumption is not necessary to the intussusception-theory, and it is probably even inadmissible.

The following instances will serve to illustrate the foregoing considerations.

A simple case is offered by the induced movement of the stamens of the Cynareæ (p. 692). When at rest, the cells of the filaments are expanded in the direction of their length, and are turgid; on stimulation, the cells suddenly shorten and become flaccid, having lost a portion of their cell-sap. The expanded state is regained by the gradual expansion of the cells, turgidity being restored by the absorption of water.

In the foregoing case, all the cells of the motile portion are affected; but in many cases some only of the cells are affected. Thus, in the case of the leaf of the Sensitive Plant, the primary petiole, when at rest, stands out nearly at right angles to the stem (Fig. 472, p. 690): on stimulation, it sinks downwards so as to form an acute angle with the internode below its insertion. The mechanism is this: when at rest, the cells of the pulvinus are all turgid, and they support the petiole in its normal position: on stimulation, the cells of the lower portion of the pulvinus lose their turgidity, water escaping from them into the intercellular spaces; these cells, being flaccid, are unable to counteract the downward pressure of the still turgid cells of the upper half of the pulvinus, and to support the weight of the leaf; consequently the primary petiole sinks downwards. The same mechanism obtains in the movements of the leaflets and of the secondary petioles; the only difference being that, in the pulvinus of a leaflet, it is the cells of the upper half of the pulvinus which lose their turgidity on stimulation, so the leaflet is raised upwards; and, in the pulvinus of the secondary petiole, it is the cells of the inner half which lose their turgidity, so the secondary petioles approach the middle line. This account is also applicable to all side-to-side movements, such as that of the leaf of Dionæa, and that of the stamens of Berberis and Mahonia.

The heliotropic or other curvatures taking place in the elongating region of growing cellular members, are due to the shortening of the cells on the side becoming concave, and to the elongation of the cells on the side becoming convex. The mechanism of the curvature seems to depend in this case not so much upon a difference of turgidity between the cells of the two sides as upon a difference in its effect: whereas turgidity induces the usual longitudinal elongation of the cells of the convex side, it induces longitudinal shortening in the cells of the concave side in consequence of extension in the other dimensions.

Turgidity is then the main factor in the mechanism of the movements of cellular members; its mechanical importance is further strikingly illustrated by the great rigidity of turgid members, and by the great force, equivalent in same cases to twenty times the atmospheric pressure, which they develope in opposition to external resistance, as when the roots of trees cause the splitting of walls or of pavements. Although one essential factor in turgidity (see p. 668) is the purely physical osmotic activity of substances in the cell-sap, it must not be forgotten that it also depends upon the resistance offered by the protoplasm to filtration under pressure: so that the maintenance of turgidity is after all a vital act. The maintenance of turgidity appears, in fact, to depend upon a certain state of molecular aggregation of the protoplasm lining the cell-wall, in which it offers resistance to the escape of the cell-sap; whereas in the flaccid condition the state of molecular aggregation of the protoplasm is such that it readily permits the escape of the cell-sap under the elastic pressure of the cell-wall.

Whilst the fundamental mechanism of the movement of mature motile members and that of growing members is essentially the same, there is this secondary difference between the two cases. The change of position which is the result of the movement of mature members, is reversible ; they can return to their former position : the change of position, curvature for instance, of growing members is reversible only so long as it has not been rendered permanent by actual deposition of substance. Thus the changes of position due to the nutation (p. 741) of growing members are only temporary, for they are of brief duration ; but changes of position due to some directive influence acting for a considerable time become permanent, for instance, the light-positions (p. 748) assumed by growing members.

The general conclusion to be drawn from the consideration of the phenomena of movement is that motile protoplasm may be in one of two states of aggregation ; either in the *state of expansion*, or in the *state of contraction* ; and that it is capable of passing from the one state to the other: in fact the term "motility" simply means the property in virtue of which the protoplasm can change its state of aggregation. In the case of cellular members, the state of expansion is that in which the protoplasm is impermeable to the cell-cap, and the cell is turgid ; whereas the state of contraction is that in which the protoplasm is permeable to the cell-sap, and the cell is consequently flaccid. The state of expansion may be regarded as the normal condition : the state of contraction is a more or less sudden deviation from this condition, the result of the action of internal or external causes ; of internal causes, as in the case of the spontaneous movements ; of external causes, as in the case of the induced movements.

This account of the mechanism of the movement of cellular members applies equally to the production of the root-pressure (see p. 701) and to the opening and closing of the stomata (see p. 698).

The ultimate point to be considered is the conception to be formed as to the nature of the change of state of the protoplasm. It has been ascertained that, in the more striking cases of induced movements, such as those of the leaves of the Sensitive Plant, the passage from the state of expansion to that of contraction is accompanied by a rise of temperature, and by certain electrical phenomena : this indicates that it is intimately connected with some catabolic process. It appears probable that the rapid passage from the expanded to the contracted state is determined by the sudden explosive decomposition of some complex substance. In the spontaneous or automatic movements, the decomposition takes place spontaneously; in the induced movements, the decomposition is determined by the action of the stimulus. Though the phenomena in question have only been observed in cases in which the contraction is sudden and violent, yet the explanation is applicable to all cases of contraction. It appears, therefore, that all movements associated with contraction are attended by a dissipation of energy in the form of heat and electricity. During the gradual resumption of the expanded condition, a process of anabolism probably goes on which leads to the formation of a fresh quantity of the decomposable substance, in consequence of which the protoplasm again becomes irritable and capable of performing another movement.

The effect of various external conditions, such as exposure to light, long-continued darkness, deprivation of oxygen, etc., in retarding or inhibiting movement, may be ascribed generally to an interference with the motility of the protoplasm, and more especially to an interference with the change in its state of aggregation upon which the variation in turgidity, leading to movement, depends. For instance, the retardation of the rate of growth by light, is the result of a diminished degree of turgidity as is proved by the diminution of the tissue-tensions. The arrest of movements of variation by darkness is probably to be ascribed to the suppression of the chemical processes active in the formation of substances upon the presence of which the passage of the protoplasm from the state of expansion to that of contraction depends: and it may be that the effect of light in inducing the condition of phototonus (see p. 760) is due to its influence in promoting these chemical processes.

In conclusion, the mechanical work done in connexion with movement remains to be considered, especially in relation to cellular members. In the movement of such a member, the work is done by those cells whose protoplasm is in a state of expansion, not by those whose protoplasm is in a state of contraction. This is a point of special physiological interest; for, on analogy with animals, the contrary might be assumed to be the case. For instance, the great force which can be exerted by a root (see p. 763) is the outcome of the turgidity of its cells, that is, of the expanded condition of their protoplasm. Similarly, in the induced movement of the leaf of a Sensitive Plant, the work is done, not by the flaccid, but by the still turgid cells of the pulvinus; and the leaf is eventually raised to its normal position by the gradual resumption of turgidity, that is, of the expanded condition of the protoplasm, by those cells of the pulvinus which had become flaccid as the result of the assumption of the contracted state on stimulation.

CHAPTER IV.

SPECIAL PHYSIOLOGY OF REPRODUCTION.

§ 18. **Introductory.** It has been already stated (see pp. 3, 67, 670) that reproduction consists essentially in the throwing off by the individual of a portion of its protoplasm which does not merely grow but developes into a new organism; and that two modes of reproduction, *vegetative multiplication* and *spore-reproduction* may be conveniently distinguished, though they are not absolutely distinct.

Reproduction has been considered so far mainly from the morphological standpoint, and it now remains to discuss it from the physiological point of view. The most important general consideration is that reproduction is a function of embryonic, as distinguished from adult, protoplasm. But it must not be overlooked that all embryonic protoplasm is not necessarily reproductive: and it is interesting to trace the differences in this respect, presented by various kinds of embryonic protoplasm. To begin with, there is no doubt (1) that the merismatic cells of the cambium are embryonic (see p. 18); but they are not at all reproductive, for they cannot give rise to a new member, still less to a new organism; they can only add to the bulk of the body of which they form part, by the development of new tissue. (2) Again, the protoplasm of a growing-point is embryonic, but it is only imperfectly reproductive; it possesses this property to the extent that it not only contributes to the increase of the member to which it belongs, but also developes new members. Finally, the protoplasm of a reproductive cell, such as a spore, is embryonic and is completely reproductive; for it does not in any degree contribute to the bulk of the parent-organism, but gives rise to a new individual.

Whilst the embryonic character of cytoplasm is probably dependent upon the presence of a large proportion of kinoplasm (see p. 95), there is at present no means of distinguishing by inspection between merely histogenic and truly reproductive cytoplasm.

§ 19. **Vegetative Multiplication.** This mode of reproduction is distinguished as *vegetative*, because it is carried on by the vegetative organs of the plant, and, in the simpler cases, it is not distinguishable from the ordinary processes of growth; though, in its higher forms it approximates to reproduction by spores. The simpler cases refered to are those of unicellular organisms: these, when they have reached by growth their characteristic limit of size, undergo cell-division, with the result that each new cell constitutes a new individual: here, multiplication is effected by a purely vegetative process, which, in a multicellular plant, would merely result in an increase in the number of the cells of which the individual consists. Much the same thing occurs in higher plants when (as in many Bryophyta, and in rhizomatous Pteridophyta and Phanerogamia) the main shoots die away, and the isolated lateral branches constitute new independent individuals. Something of a similar kind also takes place in the artificial multiplication of plants by means of cuttings: in many plants, but by no means all, if a shoot be cut off and be kept under favourable circumstances with its cut end in suitable soil, the cutting will complete its segmentation by the development of roots, and will then be a new individual. Not uncommonly, certain parts of the body may become more or less specially modified to effect vegetative propagation: for instance buds become developed into bulbs or into bulbils (see p. 68), or portions of the stem or the root become tuberous. But the specialisation which may be regarded as the highest of all, because it approaches most nearly to spore-reproduction, and involves the entire development of all the the new members, is that of gemmæ in which the vegetative reproductive body is not merely a modified member of the parent, but is a special development consisting in some cases of only a single cell (*e.g.* gemmæ of some Algæ and Liverworts, p. 67; oidium-cells of Fungi, p. 274). Something of the same kind occurs amongst the higher plants, such as some Ferns, Bryophyllum, etc., where an entirely new structure, a bud, is developed on the leaf, and produces stem, leaves and roots; it is in this way that Begonias are artificially propagated.

An interesting artificial mode of vegetative propagation is that known as *grafting* or *budding*, in which a young shoot or a bud, termed the *scion*, of one plant is inserted into the stem of another, though allied plant, the *stock*. Generally speaking, though the scion and the stock grow together so as to form one plant, they do not affect each other, the scion retaining its own peculiar characters (*e.g.* grafting of fruit-trees, budding of roses). But it is affirmed that in some cases the scion and stock do mutually effect each other, giving rise to shoots which present a mixture of their respective characters: such are termed *graft-hybrids.*

An important fact connected with vegetative reproduction is that it is associated with a rejuvenescence of the protoplasm. For example, when an adult cell of a unicellular plant, such as Pleurococcus (Fig. 166, p. 236) divides, it gives rise, not to adult cells, but to young ones: and a cutting produces a young plant, not an old one.

The relation of vegetative reproduction to the alternation of generations is of importance. In the lower plants (*e.g.* Thallophyta and Bryophyta) where the gametophyte is the conspicuous generation, it is this generation which multiplies itself vegetatively, although vegetative reproduction of a somewhat different kind has been artificially induced in the sporophyte of some Mosses (p. 362); but in the Phanerogamia it is exclusively the sporophyte which thus multiplies itself. In the Pteridophyta, whilst vegetative multiplication of the sporophyte is common, the gametophyte still retains this capacity in certain cases (some Ferns, p. 403; Lycopodium, p. 425). Vegetative multiplication does not, as a rule, affect the alternation of generations, each generation producing its like: the exceptions are afforded by cases of apogamy and apospory (see p. 87), in which the one generation is developed vegetatively from the other; that is, vegetative propagation replaces spore-formation.

§ 20. **Spore-Reproduction** (see p. 68). The highest degree of reproductive capacity is that possessed by spores. Though they are single cells, they are nevertheless capable, each by itself, of giving rise to a plant-body which, as in the higher plants, may present complete morphological and histological differentiation.

The transition from vegetative propagation, through the unicellular gemmæ, to the simpler forms of spore-reproduction is so gradual that it is difficult in many cases to distinguish them. But there is one fact which may often serve as a criterion, and that is that, at least in the lower plants, the spores are much more resistent to unfavourable external conditions, such as drought and extremes of temperature, than are gemmæ. This is due partly no doubt to the firmer cell-wall of spores, but mainly to a difference in the condition of the protoplasm in the two cases: for gemmæ are especially adapted for rapid propagation under favourable conditions. In fact the main object attained by spore-reproduction is the maintenance of the species through a period of conditions which would be fatal to the life of the individual plant.

In Phanerogams, in which the conditions of spore-formation are peculiar (see p. 431), the function of maintaining the species through a period of unfavourable conditions is transferred to the seeds which, like the spores of lower plants, have a great capacity for endurance.

Most plants, and probably all, produce spores; and from the physiological point of view there are two modes of origin of spores (p. 69): they are developed either *asexually* or *sexually*. In the lowest plants (*e.g.* Cyanophyceæ, Schizomycetes, etc.), as also in others which have become sexually degenerate (Fungi, such as the Æcidiomycetes and Basidiomycetes), spores are only produced asexually: whereas in sexual plants there is a sexual formation of spores, either exclusively (some Algæ, such as the Conjugatæ, the Fucaceæ, and the Charoideæ), or, as is more commonly the case, together with asexual spore-formation. In the higher sexual plants (Bryophyta, Pteridophyta, Phanerogamia) asexual spore-formation is entirely restricted to the sporophyte; whilst in the lower plants in which an alternation of generation can be traced (*e.g.* most Algæ and Fungi) the gametophyte retains the capacity of multiplying itself by the asexual formation of spores which are distinguished as gonidia (see p. 220). The essential difference between gonidia and asexually-produced spores is emphasised by the fact that whereas the former serve merely to reproduce the organism producing them, that is the gametophyte, or some form of it when it is polymorphic, so that the alternation of generations is unaffected, the latter only give rise to the antithetic form in the alternation of generations, that is, to the gametophyte.

The retention by the gametophyte of the lower plants of the capacity for reproduction by gonidia is of special interest in that it throws light upon the course of evolution of sexual from primitive asexual forms. Thus, the lowest Algæ are asexual, reproducing themselves solely by asexually produced spores often of the nature of zoospores. But in the course of evolution (see p. 226) some of these zoospores developed into sexual reproductive cells (gametes), whilst others remained simply zoospores; so that the plant becomes a gametophyte still possessing the capacity of reproducing itself asexually by zoogonidia, though in some forms (Conjugatæ, Fucaceæ, Charoideæ) this capacity has entirely disappeared.

The evolution of the entirely asexual sporophyte is to be traced to the advantage gained by the development of more than a single organism from the sexually-produced spore, that is, by *polyembryony.* Thus in Vaucheria and Chara the oospore gives rise directly to a single sexual individual, and the oospore is all that represents the sporophyte in the life-history of these Algæ; and this applies also to Fucus, but here a multiplication of individuals is attained by the development of eight oospheres in the oogonium. A rudimentary form of polyembryony is presented by the Desmids where the zygospore gives rise to two individuals. It is more marked in such plants as Sphæroplea and Œdogonium, where the oospore gives rise to several (2–8) zoospores from each of which a new sexual individual is developed: here the oospore and its zoospores represent the sporophyte. The sporophyte first makes its appearance as a distinct cellular organism in Coleochæte (p. 250), and from this point onwards its further evolution can be readily traced through the sporogonium of the Bryophyta to the Pteridophyta and Phanerogamia where it is the predominant form in the life-history. The sporophyte is thus essentially *gamogenic*, that is, it is developed as the result of a sexual process (p. 69).

Whilst in the majority of cases the sporophyte is developed from a sexually-produced spore, it is sometimes developed from the fertilised female organ; this is the case in plants in which there are either no differentiated gametes (*e.g.* Eremascus, p. 297), or no differentiated female gamete (*e.g.* Rhodophyceæ, p. 269); but it is still the product of a sexual process. In some cases of sexual degeneration (*e.g.* apogamous Ferns, p. 378; Ascomycetes, p. 298) the sporophyte is developed vegetatively (p. 87).

The sexual formation of spores is the result of the fusion of two sexual reproductive cells or gametes, neither of which is, as a rule, capable by itself of developing into a new individual; though, in some of the lower plants in which sexual differentiation is incomplete (*e.g.* Ulothrix, Ectocarpus; see p. 226) the gametes may germinate independently. The act of fusion is a sexual process, and the result is a cell (oospore or zygospore, p. 80) which proves itself to be a spore by developing into a new individual which, in all plants presenting alternation of generations, is the sporophyte.

In some cases the spore is formed from a gamete without any sexual process, that is, *parthenogenetically* (p. 87); this applies to the imperfectly sexual gametes of Ulothrix and Ectocarpus mentioned above, whence it follows that there can be both male and female parthenogenesis; to the azygospores of some Zygomycetes (pp. 288, 290); to the oospores developed in the oogonia of the Saprolegniaceæ (p. 294), and to that of *Chara crinita* (p. 254).

It has been ascertained, in plants other than the Thallophyta, that the nucleus of the sexually-produced spore contains twice as many chromosomes (p. 119) as does that of either of the gametes; for instance, if the number of chromosomes in the nucleus of the gamete be twelve, that in the nucleus of the oospore will be twenty-four; and since the sporophyte is developed from the oospore, the number of chromosomes in the nucleus of each of its cells is also twenty-four, and is twice as great as that in the nucleus of the cells of the gametophyte. But, since the gametophyte is *agamogenic*, being developed from the asexually-produced spores of the sporophyte, the question arises as to how this reduced number of chromosomes is arrived at. It is simply due to the fact that when the nucleus of a spore-mother-cell is about to divide, the fibrillar network breaks up into only half the number of chromosomes characteristic of the sporophyte (for instance, twelve instead of twenty-four); hence the spore, when formed, contains the reduced number of chromosomes characteristic of the gametophyte and is, in fact, the first term of that generation.

These points have not yet been fully investigated in the Thallophyta, in which group various special questions arise. For instance, as already pointed out, in many of these plants the gametophyte is directly developed from the sexually-produced spore, and yet there can be little doubt that the nuclei of the gametophyte each contain only half the number of chromosomes present in the nucleus of this spore; for, were it otherwise, each sexual act would involve the doubling of the number of the chromosomes in the nuclei of the succeeding generation, and by continued repetition of the process the number would become indefinitely large. It seems probable that a reduction in the number of the chromosomes takes place early in the germination of the sexually-produced spore. Thus it has been observed in certain Desmids that the nucleus of the germinating zygospore divides into four, but the product is only two new individuals each with a single nucleus; and similarly, that the nucleus of the zygospore of Spirogyra divides into four, yet the unicellular embryo contains but a single nucleus. Then there is the further question as to the number of chromosomes in the nuclei of the gonidia and in those of parthenogenetically produced spores; and the phenomena of apogamy and apospory in the higher plants also require investigation from this point of view.

§ 21. **Sexual Reproduction.**—The sexual process consists typically, though not exclusively (see pp. 225, 275) in the fusion of two gametes, that is, of two sexual reproductive cells, and it is to this typical case only that reference is here made.

The process consists essentially in the fusion of the homologous parts of the gametes. In the Phanerogams, in which the process has been most minutely investigated, it is briefly as follows:—The male gamete, being smaller and more active than the female, enters the latter (see Figs. 298, 302); then the centrospheres of the two gametes fuse, and then their nuclei, male nucleus (or pronucleus) with female nucleus (or pronucleus), to form the nucleus of the oospore, and with that the process is complete. But the fusion of the nuclei is not accompanied by any fusion of their respective chromosomes; these remain distinct, so that there are twice as many of them as in the nucleus of either gamete: but when the oospore begins to germinate, the first division of its nucleus takes place in such wise that each half receives an equal number of chromosomes derived from each of the sexual nuclei. No doubt the process is essentially the same in all other cases.

The first question which naturally arises is as to the nature of *sexuality*; the question, namely, as to what difference, if any, can be observed between a gamete and an asexually-produced spore. To this question no answer can at present be given; no difference can be detected between a gamete and a spore; in all plants in which the matter has been investigated, in a Fern, for instance, it is now known that the number of chromosomes in the nucleus is the same in the gamete as in the spore.

It was thought that there was an essential observable difference between a gamete and a spore, of this nature, that the nucleus of the gamete contained fewer chromosomes than did that of the spore. It had been observed in many cases that, as part of the development of a gamete, a portion of the protoplasm of the mother-cell was thrown off as a *polar body* (see p. 82), and it was concluded that this involved the reduction by half in the number of chromosomes in the nucleus of the gamete, and thus caused it to differ materially from a spore. But this view is no longer tenable in face of the fact that the reduced number of chromosomes in the nucleus is characteristic, not only of the gametes, but also of the whole gametophyte, and in fact of the spore itself also (see p. 771). The polar bodies can now only be regarded as sister-cells of the gametes and as equivalent to them, though not functional.

It must not, however, be concluded that because there is no *observable* difference between a gamete and an asexually-produced spore, there is no difference whatever between them; on the contrary it is clear that they differ widely, since the former cannot (except in the rare cases of parthenogenesis), whilst the latter can, develope into a new organism.

The second question is as to the nature of *sex*: what is the difference, if any, between a male and a female gamete? In some cases there is a marked external difference; for instance, in the Pteridophyta, Bryophyta, and many Algæ, the female gamete is a large motionless oosphere, whilst the male gamete is a small actively-swimming spermatozoid. But this marked difference is not essential, it is merely adaptive; it is an adaptation to a more or less aquatic mode of life or, at least, of fertilisation. Moreover, it is obviously inapplicable in explanation of the many cases in which the two conjugating gametes are externally quite similar (isogamous plants, see p. 80). Nor has minute microscopic investigation brought to light any distinguishing criterion. But it must not be concluded on this account that there is no difference between a male and a female gamete; it is obvious that there is an essential physiological difference between them. For, were it otherwise, it would be impossible to account for such a fact, for instance, as that even where, as in many Algæ, the gametes are all extruded into the water, fusion never takes place between two male or two female gametes, but only between a male and a female.

Brief allusion may be made to the means by which the sexual process is ensured. It might be thought that the most effectual means would be the development of the male and female organs in close propinquity on the same individual. No doubt this is the case, but the result is to ensure the less advantageous mode of the process, the mode of self-fertilisation; in fact, in many cases in which the male and female organs are thus developed close together as in monœcious plants (p. 86), self-fertilisation is prevented by dichogamy (for instance, the prothallia of Ferns, p. 399). The real problem is, then, to ensure a sexual process between two gametes derived from distinct individuals. The end is attained either directly, by bringing the diverse gametes together; or indirectly, by bringing the spores together, and consequently also the gametophytes.

The method of bringing the two gametes together is essentially connected with the aquatic mode of fertilisation. It has been observed and investigated in plants in which, whilst the oosphere is motionless and remains in the female organ, the spermatozoids are free-swimming; and it is among the most striking phenomena of chemiotaxis (see p. 755). In various Mosses and Ferns it has been ascertained that, on the opening of the archegonium, the mucilage which is extruded includes some substance which diffuses into the water and attracts to the archegonium any spermatozoid that may be present; in Mosses the substance in question is cane-sugar; in the Ferns, a salt of malic acid.

The method of bringing the spores together, so that they may germinate near each other, is especially characteristic of heterosporous plants, and more particularly of those which grow erect on dry land. It is thus most strikingly exhibited by the Phanerogams, where the microspores are carried by the wind or by insects into such a position that they germinate in proximity to the macrospores (see p. 452). But it is not confined to land-plants, for it occurs, as the result of a remarkable adaptation, in Azolla (see p. 411). Nor is it exclusively restricted to heterosporous plants, for cross-fertilisation in the Ferns and Mosses is largely dependent upon the propinquity of a number of gametophytes developed from spores shed without being scattered.

Sexual Affinity. This term is used to express the fact that a certain relationship must exist between any two gametes of opposite sex in order that a sexual process may take place between them; when the limit is overstepped in the direction of either a too close or a too remote relationship, the process will either not take place at all, or the offspring will be few and feeble.

The most fertile sexual process is that taking place between the gametes of different individuals of the same species. It has been proved that the offspring of such *cross-fertilisation* have the advantage in vigour and fertility over the progeny of one of the same plants when self-fertilised. It has, in fact, been proved that in many Phanerogams the pollen of a flower is incapable of fertilising the oospheres of its own ovules; and that the pollen from another flower of the same plant is only slightly, if at all, more potent.

A sexual process may also take place between the gametes of varieties of the same species; of distinct species of the same genus; and even of species belonging to different genera. Such a process is known as *hybridisation*, and the progeny as *hybrids*, the hybrid being distinguished as a variety-hybrid, species-hybrid, or genus-hybrid, according to circumstances (see p. 457).

Hybridisation has been but imperfectly investigated in the Thallophyta, but it is known to take place between *Fucus serratus* ♂ and *F. vesiculosus* ♀ : in the Mosses some species-hybrids are known, and a few genus-hybrids (between the allied genera Physcomitrium and Funaria; *F. hygrometrica* ♂ × *P. pyriforme* ♀) : in the Ferns variety-hybrids are common, and several species-hybrids are known: in Phanerogams variety-hybrids and species-hybrids are common, and several genus-hybrids are known (*e.g.* between Verbascum and Celsia; Brassica and Raphanus; Galium and Asperula; Campanula and Phyteuma; Gymnadenia and Nigritella; Epiphyllum, Cereus, and Phyllocactus). Species-hybrids are usually designated by a combination of the specific names of their parents; as, for instance, *Digitalis purpureo-lutea*, the hybrid resulting from the fertilisation of *D. lutea* with pollen of *D. purpurea*. When it is desired to state accurately which is the male and which the female, such an expression as *Verbascum Lychnitis* ♀ × *phœniceum* ♂ is used.

Hybridisation is by no means equally common in all families; thus, among Phanerogams, whilst it is common in such orders as the Compositæ, Scrophulariaceæ, Polygonaceæ, Salicaceæ, and Orchidaceæ, it is comparatively rare in the Cruciferæ and Labiatæ, and quite exceptional in the Umbelliferæ and Leguminosæ. And within the limits of any one natural order the capacity for hybridisation is not the same in all genera; thus, in the Geraniaceæ, the genus Pelargonium possesses it in a high degree, whilst Geranium and Erodium do not; in the Caryophyllaceæ, Dianthus readily hybridises, but Silene does not; and in the Iridaceæ the same contrast exists between Gladiolus and Crocus; and the same applies to the various species of any given genus. Nor are all hybridisations equally fertile as estimated, in Phanerogams, by the number of sound seeds produced, and by the vigour and fertility of the resulting hybrid-plants; the general rule being that the more remote the two species hybridised, the more delicate and the less fertile will be the offspring, and in fact many hybrids are altogether sterile; in any case they are more fertile with pollen from one of the parent-forms than with that of other similar hybrids. It is only when the relation between the parents is such as to ensure the appropriate degree of sexual affinity that the product of the union is a vigorous and fertile progeny.

It is the rule that hybridisation is *reciprocal*; that is, that if the oospheres of a species A can be duly fertilised by the male gametes of a species B, the oospheres of the species B are equally susceptible of fertilisation by the male gametes of the species *A*. But this is by no means always the case. Thus *Mirabilis Jalapa* can be fertilised by the pollen of *M. longiflora*, but the converse crossing has not yet been effected; similarly the cross *Nymphæa cœrulea* ♀ × *N. capensis* ♂ has taken place, but not the cross *N. capensis* ♀ × *N. cœrulea* ♂; and the cross *Fucus vesiculosus* ♀ × *F. serratus* ♂, but not *F. serratus* ♀ × *F. vesiculosus* ♂. It also happens that even when hybridisation is reciprocal, the one union (*A* ♀ × *B* ♂) is more fertile than the other (*B* ♀ × *A* ♂); thus the cross *Dianthus barbatus* ♀ × *D. superbus* ♂ is more fertile than the cross *D. superbus* ♀ × *D barbatus* ♂; and again *Digitalis lutea* ♀ × *D. ambigua* ♂ than *D. ambigua* ♀ × *D. lutea* ♂.

These cases of non-reciprocal, or of imperfectly reciprocal hybridisation, seem to be at variance with the statement that fertile hybridisation is dependent upon sexual affinity; for if this be true, why is it that the cross *A* ♀ × *B* ♂ should succeed, but not the cross *B* ♀ × *A* ♂, the sexual affinity being necessarily the same in both cases? The failure of the cross in these cases is partially due to purely mechanical reasons; for instance, whilst *Mirabilis Jalapa* is fertilised by the pollen of *M. longiflora*, *M. longiflora* cannot be fertilised by the pollen of *M. Jalapa*, probably because the pollen-tubes of the latter are unable to grow long enough to reach from the stigma to the ovule of the former species. All these cases require further investigation.

Effects of the Sexual Process. The sexual process is not always limited in its effect to the production of a spore which will give rise to a new individual. For instance, when the female cell is borne by the parent at the time of fertilisation, the act of fertilisation induces a more or less marked growth and change in the adjacent organs and tissues of the parent, leading to the formation of a *fruit* (see pp. 88, 528). But further than this, it has been occasionally observed in Phanerogams that the constitution of the mother-plant is somewhat modified in consequence of pollination by another form. For instance, in the Maize, whilst the grains in the fruit-spike of the mother-plant usually have the colouration peculiar to the mother, from whatever source the pollen may have been derived, it sometimes happens that when a plant whose grains are normally yellow or white is pollinated from another variety whose grains are brown or blue, the resulting grains are brown or blue. It is well known that, in Orchids, the pollination of the stigma acts as a stimulus to the development of the ovary and ovules: and in some cases it appears that even fertile seeds may be produced simply by the influence of pollination, the mother-plant being stimulated to produce seeds without any sexual process, that is, parthenogenetically (*pseudogamy*).

Somewhat analogous to these phenomena are those presented by the so-called *graft-hybrids* (see p. 768), in which scion and stock seem to mutually affect each other. For instance, the Bizzaria-Orange is a tree which bears branches and fruits characteristic of *Citrus Aurantium* and *C. medica*, and of an intermediate form, and is stated to be a graft hybrid of these two species; similarly *Cytisus Adami* is a plant possessing characters intermediate between those of *Cytisus Laburnum* and *C. purpureus*, and is stated to be a graft-hybrid of *C. purpureus* on *C. Laburnum*; but since the evidence that these plants really are graft-hybrids is inconclusive, it is unnecessary to consider them further.

§ 22. **Heredity and Variation.** The term *heredity* is used to express the fact that an organism inherits in some degree the characters of its parent or parents. The degree of heredity—that is the degree of resemblance between offspring and parents—varies widely, inasmuch as not all the characteristics of the parent are hereditary in all modes of reproduction. The highest degree of resemblance is attained by means of vegetative propagation: by this means the peculiar features of the individual may be exactly reproduced in the offspring, and consequently it is extensively made use of in horticulture (*e.g.* propagation by cuttings and bulbs; budding of Roses; grafting of fruit-trees, and of ornamental trees and shrubs with variegated or otherwise abnormal foliage, etc.) to perpetuate some specially valuable peculiarity of a plant, and to multiply the number of individuals possessing it. Such a high degree of resemblance between parents and offspring cannot be attained by means of sexual reproduction, for many of the peculiar characteristics of the parents are not transmitted by this means. The plants resulting from a sexual process between two individuals of the same variety or species present, not so much the characteristics of the parents, as the characters of the variety or species.

The phenomena of heredity in connexion with sexual reproduction are especially striking in the case of hybrids, though the result of the crossing of species or varieties, as shown by the characters of the progeny, is by no means always the same. Whilst it is true, as a rule, that hybrids are intermediate in character between the species or varieties to which their parents respectively belong, this is by no means always the case; for some hybrids resemble the one parent more than the other, either in external form and colour, or in properties such as resistance to cold, time of flowering and fruiting, etc.: in fact, when, for instance, a number of seeds are produced by hybridisation, none of the resulting seedlings may be intermediate in character between the two parents, but some may quite resemble the one parent, and the remainder the other. When the hybrids are intermediate in character, the blending of the parental features may manifest itself in different degrees; it may be slight, as for instance when a hybrid of parents with differently coloured flowers, bears flowers of the two distinct colours: or more intimate, as when in such a case the hybrid bears flowers with blotches or stripes of the two colours; or complete, as when in the same case the flowers of the hybrid are of a tint intermediate between the colours of the parental flowers. The same peculiarities are presented, of course, by other structures; for instance, as regards the colour, size, flavour of fruits, the size and shape of leaves, etc.

One of the most remarkable aspects of heredity in plants is its relation to the alternation of generations. When the life-history of a plant presents a regular alternation of sporophyte and gametophyte, it is the alternate, and not the successive, generations which resemble each other; sporophyte resembling sporophyte, gametophyte resembling gametophyte. The hereditary characteristics of the sporophyte, for instance, are not presented by the gametophyte, which, though it springs from it, is commonly an altogether dissimilar organism, but are transmitted through the gametophyte to the succeeding gamogenic sporophyte. This is not only obviously the case in plants, such as Ferns, in which the alternate generations are distinct organisms; but it is equally true of the plants, such as Bryophytes and Phanerogams, in which the alternate generations remain more or less intimately connected.

Variation is the term used to express the fact that an organism may differ more or less widely from its parent or parents, presenting often some altogether new characters.

It is in connexion with sexual reproduction that variation is most frequently manifested. It may, in fact, be generally stated that variation is more frequent and more marked, the more remote (within the limits of sexual affinity) the relationship between the two parents: thus variation is most common in the offspring of individuals of different species; frequent in the offspring of two individuals of different varieties of the same species; least common in the offspring of two individuals of the same species or variety.

It would seem natural to carry this rule further, applying it to the case of asexual reproduction so as to lead up to the conclusion that variation does not occur at all in plants produced asexually; that variation is, in fact, necessarily associated with the sexual process; a conclusion which has met with a certain measure of acceptance. But it is a question whether this conclusion can be fairly drawn when all the facts of reproduction in plants are duly taken into account. Considering, first, the fact of asexual reproduction by means of gonidia, which is so common among the Thallophytes, and which in some Fungi (*e.g.* Basidiomycetes and many others), is the only known mode of reproduction, it is inconceivable, in the face of the vast number of families, genera, and species of the plants under consideration, that variation has not taken place among them, although they present no indications of sexuality. Then there are the facts of *bud-variation* to be considered. Bud-variation is the term used to express the fact that shoots, whether reproductive or vegetative, are sometimes developed, which differ in some striking manner from the other normal shoots of the plant; these varying shoots are known as "sports": for instance, many varieties of Rose are known to have arisen in this way, such as the Moss-rose from the Provence rose (*Rosa centifolia*). The varieties arising in this way can, as a rule, only be propagated vegetatively, by cuttings, grafts, etc., but occasionally they come true from seed. Here again variation seems to occur independently of sexual reproduction.

With regard to the causes of variation, it would appear that the capacity for variation, or *variability*, is increased (*a*) by sexual reproduction, and (*b*) by external conditions, more particularly high nutrition, as is shown by the fact that bud-variation, for instance, is rare in wild plants but comparatively common in cultivated plants. The character of the variation has also to be considered. There is no doubt that variation is often the manifestation, not of a new character, but of an old ancestral character which had become dormant: this is especially true of the variations of sexually-produced plants, but it is also true in many cases of bud-variation: this kind of variation is termed *reversion*. But there seem to be many cases of variation, and more particularly of bud-variation, which cannot be attributed to reversion, and in which the direction of variation does not appear to be traceable to any determining external causes: such variations seem to be altogether fortuitous.

The Origin of Species. From the foregoing statements relating to heredity and variation, it is possible to draw conclusions not only as to the maintenance of existing species, but also as to the evolution of new species.

It is clear that new forms may arise in either of two ways:—(1) either, first, as the result of the crossing of distinct varieties or species; many recognized species and varieties are probably of hybrid origin: (2) or, second, as the result of variation. The forms thus produced will exist, for a time at any rate, provided that they are capable of reproducing themselves, either vegetatively (*e.g.* by tubers, bulbs, etc.), or sexually (by seeds, etc.) But their persistence for any long period depends upon their success in the struggle for existence. They have to compete for their life with their parents and with any other closely similar new forms which may have also been developed: if they are successful, they will persist, and their competitors will, some or all of them, die out. The degree of their success depends essentially upon the degree of their adaptation to the circumstances amidst which they have to live. If they excel any of their competitors in the combination of qualities (such as hardiness, time of flowering or fruiting, fertility, etc.) which adapt them to the prevailing conditions of life, they will persist and the others will disappear. This condition of struggle constitutes *Natural Selection*, for the survivors of the struggle are, as it were, selected by the fact of their survival.

At first all new forms, however produced, appear as what may be termed varieties of their parent species: but, if they possess the requisite reproductive capacity, and if they are successful in the struggle for existence, they eventually become isolated by the disappearance of many of the allied forms, including perhaps the parent forms, and remain as distinct species. Thus in some genera of flowering plants, the recognised species are few and distinct; whilst in many genera (*e.g.* Rubus, Hieracium) the greatest difficulty is experienced in distinguishing the species and varieties, because the process of isolation by natural selection has not yet been sufficiently operative.

§ 23. **The Theory of Reproduction.** The theory of reproduction is extremely simple in connexion with the more primitive modes of vegetative propagation. When, for instance, a unicellular organism divides into two, it is easy to understand that the two new organisms will resemble each other and the parent from which they have sprung, because the parental cell divided into two exactly similar parts. Again, when a plant is propagated by a bulb or a cutting, it is still easy to understand that the resulting plant will resemble, as it usually does in detail, the plant which produced the bulb or from which the cutting was taken. But when a plant, a Mushroom for example, is developed from a single minute reproductive cell, representing but an infinitesimal proportion of the protoplasm of the parent plant, it is not easy to understand how the parental characters can be transmitted to the offspring by such apparently inadequate means. The bulk of the structure by which reproduction is effected, would seem to be an expression of the fact that the bulkier reproductive structure (bulb, tuber, etc.) is but a vegetative structure imperfectly differentiated for the purpose of reproduction, but which, at the same time, ensures a close individual resemblance between parent and offspring: whilst a single minute reproductive cell, on the other hand, such as the gonidium of a Mushroom, though a less efficient instrument of heredity, is much more highly specialised for the work of reproduction.

If it be asked in what does this specialisation consist, no satisfactory reply can be given at present; as already pointed out (see p. 766) there is no method by which reproductive capacity can be analysed or determined. It is, however, generally agreed that the transmission of hereditary characters is intimately associated with the nucleus of the reproductive cell, and especially with the fibrillar network (see p. 96) of the nucleus. But the fact that this is so still remains unexplained, as also the fact that reproductive cells differ so widely in their properties from vegetative cells, although many attempts at an explanation have been made, such as the theory of Pangenesis and that of Germ-plasm.

Whilst the ultimate facts of reproduction thus remain unexplained, the proximate facts of sexual reproduction can be rendered intelligible. It has been already pointed out (p. 770) that a gamete is incapable by itself of giving rise to a new individual; but that by the fusion of two gametes of opposite sexes a spore is formed, possessing twice as many chromosomes in its nucleus as did the gametes, from which a new individual may be developed. The nuclei of the new individual (in view of the strict equality in the process of mitotic division, p. 118) must all contain chromosomes derived from both the gametes which had fused in the sexual process; and if, as seems probable, the transmission of hereditary characters is associated with the nuclear chromosomes, the characters of the individual will be those transmitted to it by the chromosomes of the gametes. Consequently, if the gametes were derived from two distinct individuals, the characters of the new individual will be those of its two parents. In this way the more obvious phenomena of heredity can be traced to a material basis, and are thereby rendered more comprehensible.

But what is true of the new individual, applies likewise to its parents: the characters which each parent transmits to the offspring are those which it has itself received from its two parents, and so on: hence the characters inherited by any individual are to be regarded as belonging rather to the race than to its immediate progenitors. This conception also can be traced to a material basis. It has been suggested that the discoid segments (consisting of linin and chromatin, p. 96) of which the nuclear chromosomes consist, each represent, in a gamete, substance derived from a number of ancestors, the whole chromosome representing many ancestors, and the chromosomes together all the ancestors whose substance still persists in the gamete and will be transmitted by the gametes to the next generation. The term *id* is used to designate one of those material units which seem to constitute the physical basis of heredity.

Applying these considerations to the elucidation of the reproductive process in a plant, such as a Fern, whose life-history presents antithetic alternation of generations, it would appear that the sudden reduction by half of the number of the nuclear chromosomes which attends the initiation of the gametophyte (see p. 771) is to be attributed to the fusion of the ids in pairs: and further, that it is not until this stage that a real fusion of the nuclear substance of the gametes actually takes place.

The phenomena of heredity as manifested in the products of sexual reproduction may be accounted for in connexion with this fusion of the parental ids. When, for instance, in hybridisation, all the parental ids exert their full influence, the offspring is precisely intermediate in character: but when, from some cause which cannot now be explained, some of the ids are paralysed or neutralized, the offspring resembles one parent more than the other. The character of the hybrid too, whether blended or blotched, may be referred to some such cause.

Turning now to the phenomena of variation: this may be accounted for, when it depends on reversion, on the assumption that some of the ancestral ids which have remained neutralized and ineffective for generations, are, as it were, set free in consequence of some fresh crossing or of some important change in the conditions of life, so that the latent ancestral characters now reveal themselves. It is scarcely possible to offer any satisfactory explanation of variation due to other causes, but there is one point which, in conclusion, demands special consideration; that is, whether or not variations which are the result of the influence of the external conditions, can be transmitted to the offspring. There is no doubt that they can be transmitted by means of vegetative propagation. But the real question is as to whether or not they can be transmitted through the sexual process; as to whether or not the ids in the gamete of an individual can transmit not only the ancestral characters, but also characters which presented themselves apparently for the first time in the individual itself. The weight of opinion is at present in favour of the view that such acquired characters cannot be so transmitted; but in the face of the fact that some variations apparently of this nature (*e.g.* doubling of flowers, variegation of leaves) are often transmitted in this way, it cannot be conceded that this view is conclusively established.

INDEX.

PART I.—CLASSIFICATION AND NOMENCLATURE.

PART II.—MORPHOLOGY, ANATOMY, AND PHYSIOLOGY.

Butler & Tanner, The Selwood Printing Works, Frome, and London.

Rostellum – "the abortive anterior lobe of the stigma" – p 457

9

Section of Angiosperms - 431
* Epipactis - 457
Acorus calamus }- 529
Arum maculatum }

Iris - 568
× Utricularia - 647 bladders
Asclepias - 651
Lobelia - 657
× Hypogynous, Perigynous, Epigynous 4
* Epigynous flower (cucumis) section à la
. 62

Asclepias - 651
Yarrow - 663
Cypripedium calceolus 565
Wheat - 546
Capers - 605