PLANT ANATOMY

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PERGAMON PRESS

OXFORD · NEW YORK
TORONTO · SYDNEY · BRAUNSCHWEIG

CONTENTS

Pergamon Press Ltd., Headington Hill Hall, Oxford
Pergamon Press Inc., Maxwell House, Fairview Park, Elmsford, New York 10523
Pergamon of Canada Ltd., 207 Queen's Quay West, Toronto 1
Pergamon Press (Aust.) Pty. Ltd., 19a Boundary Street, Rushcutters Bay, N.S.W. 2011, Australia
Vieweg & Sohn GmbH, Burgplatz 1, Braunschweig

First English Edition 1967
Reprinted with corrections 1969
Reprinted 1972

Original Hebrew book published by
Hakkibutz Hameuhad Publishing House Ltd.

Library of Congress Catalog Card No. 66-24822

Printed in Great Britain by A. Wheaton & Co., Exeter

08 011943 3

PREFACE

PLANT anatomy is a basic science and as such is of great importance to students of all the plant sciences. Without a thorough knowledge of this field the physiological processes carried out within the plant and the phylogenetic relationships between the various plant groups cannot be fully understood. The detailed study of the elements and tissues of which the plant is constructed enables a better understanding of adaptation to special functions as well as of the adaptation of entire plants to different environmental conditions. Without a thorough knowledge of the anatomical and histological structure of plants the results of physiological and ecological experiments, for instance, may be incorrectly interpreted. Also, to-day no conclusive opinions on evolutionary trends or taxonomic relationships can be suggested on the traditional basis of the study of external morphological characteristics alone; it is now necessary to support such work by the use of the many and varied anatomical and histological characters, which can be observed only from microscopic, and even submicroscopic, investigation.

Anatomy, which draws the attention of the student to the form, variability and structure of the tissues comprising the plant body, can be said to develop an aesthetic sense. In addition to this, the awareness of the regularity, and repetition, at different levels, of the structural patterns, as well as of the amazing correlation of structure and function, serves to make anatomy a rewarding field of research.

A large section of this book deals with the vegetative plant body. The first introductory chapter briefly presents the general structure of the higher plant. This is followed by the descriptions of the different types of cells and tissues that are present in the Tracheophyta. Later chapters describe how the vegetative plant body, both primary and secondary, is constructed of these various tissues. The last section deals with the structure of the flower, fruit and seed. In the chapter on the flower I have covered pollination, fertilization and embryo development. In my opinion this is necessary in order that a full and balanced picture of the development and structure of plants and their tissues can be obtained.

An effort has been made, when dealing with the structure of the elements, tissues and organs of the plant body, to employ the following approaches—ontogenetic, phylogenetic, physiological and ecological. Attention has also been paid, wherever possible, to such characteristics that are of importance to agriculture and industry.

In view of modern research in plant anatomy and biology as a whole, which has brought to light so many

Reproductive Organs

bility in the definitions of the various elements and tissues is stressed throughout the book.

In many cases I have endeavoured to point out problems which as yet constitute serious gaps in our knowledge, and which await further research.

The inclusion of a large number of illustrations has enabled the text to be written in a concise form. The great majority of the micrographs are original and have been made from slides in the collection of the laboratory of Plant Anatomy at the Hebrew University of Jerusalem. The drawings are in part original or have been taken from previous publications of the author, and the rest have been redrawn and adapted from various books and articles. In the case of the latter the original author is cited in the legend and the reference is given at the end of the relevant chapter or Chapter 1. In a book of this size and scope it is impossible to deal with all the relevant facts in detail and therefore many references are given in the text. It is hoped that readers will refer to these and other articles, books, etc., in order to broaden their knowledge. For convenience, details of these references are given at the end of each chapter.

This book was originally written in Hebrew for the use of students studying in Israel. Thus many of the examples cited are of plants growing in this and neighbouring regions.

I express my thanks to all those who helped me in the preparation of the original Hebrew book. I am indebted to my friend S. Stoler for his critical reading of the manuscript and for his valuable suggestions; to Mrs. Ella Werker for her great help in the preparation of the manuscript and for seeing the book through press; to Mrs. Batya Amir for the careful and accurate execution of most of the drawings; to Y. Shehori for his aid in the preparation of most of the photographs appearing in the book; and to Mrs. Irena Fertig for her assistance in reading the proofs. My thanks are also extended to all those who have put at my disposal photographs and drawings, as well as to my colleagues at the Hebrew University who gave me valuable advice at all times. I especially thank my students, throughout the years, who have encouraged me to write this book.

In connection with this revised English edition I am indebted to Dr. C. R. Metcalfe and Sir George Taylor who suggested and encouraged me to have my book translated. I greatly appreciate the criticism and advice that Dr. Metcalfe extended after having read the English manuscript. I thank Dr. F. A. L. Clowes who undertook to edit the English. I gratefully acknowledge the permission so generously granted to me by the Hakkibutz Hameuhad Publishing House Limited to translate the original text. I also thank Mrs. Sybil Broido-Altman for undertaking the translation. Once again I thank Mrs. Ella Werker, who assisted in the collation.

A. FAHN

Jerusalem,

April, 1965

CHAPTER 1

GENERAL STRUCTURE OF HIGHER PLANTS

PLANTS that bear seeds are termed spermatophytes. These plants produce *spores* (newly formed embryo sacs and pollen grains) and therefore they are sporophytes. These plants develop from a zygote which results

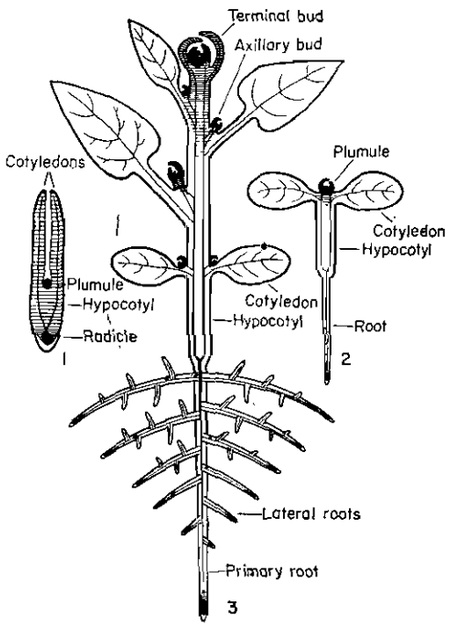

FIG. 1. Schematic drawings of longitudinal sections of a dicotyledonous plant at various ages. 1, Embryo. 2, Seedling. 3, Mature plant. (Adapted from Troll, 1948.)

from the fertilization of an egg cell by a male gamete. At the start the zygote divides into two cells which themselves undergo further divisions to form the embryo. The embryo usually consists of *radicle, hypocotyl, cotyledons* and *plumule* (Fig. 1, no. 1). The embryo remains concealed

and dormant within the seed which develops from the entire ovule. It is not always clear whether the embryo possesses a radicle proper or whether it merely has a root apical meristem. It is difficult to make a definite distinction between the radicle and hypocotyl, and therefore the axis of the embryo is called the *hypocotyl-root axis*.

With the germination of the seed the embryo renews its growth. The radicle grows and penetrates deeper into the soil. In some species the hypocotyl elongates and so raises the cotyledons above soil level where they become green (epigeal germination). In other species the hypocotyl does not elongate, or it elongates only very slightly, and the cotyledons remain below soil level where they eventually rot (hypogeal germination). The plumule, which is situated above the junction of the cotyledons to the hypocotyl, elongates and gives rise to the stem and leaves (Fig. 1, nos. 2, 3).

That part of the stem to which the leaf is attached is termed the *node* and that part of the stem between two nodes, the *internode*. The number of nodes and internodes increases with the continued growth of the stem.

At the start of germination all the cells of the embryo divide, but later cell division is restricted to certain areas of the seedling—usually in the apices of the axis.

The morphology of the various organs of the spermatophytes is extremely varied. The nature of the different organs, such as the stem, leaf, root, flower and fruit, and the differences in their external and internal structure have been variously interpreted (De Bary, 1877; Strasburger, 1891, 1923; Haberlandt, 1918; Goebel, 1928–33; Troll, 1935, 1937, 1938, 1939, 1954–57; Eames and MacDaniels, 1947; Foster, 1950; McLean and Ivimey-Cook, 1951, 1956; Esau, 1953; Eames, 1961). The stem (which bears the leaves) together with the leaves forms a single ontogenetic and, apparently, also evolutionary unit, and so these organs together are termed the *shoot*.

The shoot and root, together with their branches, form an organic continuation of the embryo as their development results form the activity of the apical meristems, which are tissues directly descended from those of the embryo.

In those spermatophytes in which the apical meristems of the main shoot remain active throughout the life of the plant, the shoots developing from the axillary buds remain secondary and the extent of their growth is regulated by the apex of the main shoot. Such branching of the stem is termed *monopodial* (Fig. 2, no. 1). The main axis and the successive axial branches do not always have the ability to grow indefinitely. In many plants the shoot apex becomes reproductive or aborts, and then further growth is carried out by lateral buds. Such branching is termed *sympodial* (Fig. 2, no. 2).

In many cases buds and roots may develop from portions of the plant distant from the apical meristems; such organs are termed *adventitious*

organs. Examples of such organs are the fibrous roots which are common among the monocotyledons and develop from the hypocotyl or from the basal internodes of the stem. Adventitious roots sometimes develop from aerial portions or from old roots of woody plants. Adventitious shoots are known to develop on roots and on stems from places in which no dormant buds are found. The apices of the adventitious shoots and roots contain the same meristematic tissues as the apical meristems of the ordinary organs of the primary axis.

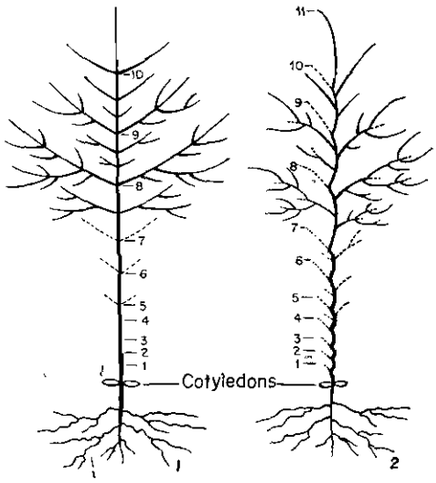

FIG. 2. Diagrams of the mode of branching in trees. 1, Monopodial branching. 2, Sympodial branching. The numbers indicate the position of the tip at the end of each annual longitudinal increment. (Adapted from Troll, 1948.)

As the cells formed by the meristem become more distant from the apex, they undergo gradual differentiation (Fig. 3). Near the apex of the shoot and root three meristems of different tissues become observable: (1) *protoderm*, from which the *epidermis*, the protective tissue, develops; (2) *procambium*, from which the primary vascular tissues *(primary xylem* which serves mainly to transport water and the *primary phloem* which serves to transport metabolites) develop; (3) *ground meristem*, from which tissues of the cortex and pith develop. These comprise *parenchyma*, the basic tissue of the plant, *sclerenchyma* and *collenchyma*, the supporting tissues of the plant.

The cells of the procambium gradually differentiate into phloem and xylem elements, and so these elements become more numerous as seen in consecutive cross-sections of the stem made at levels further away from the apex. The phloem elements [illegible]

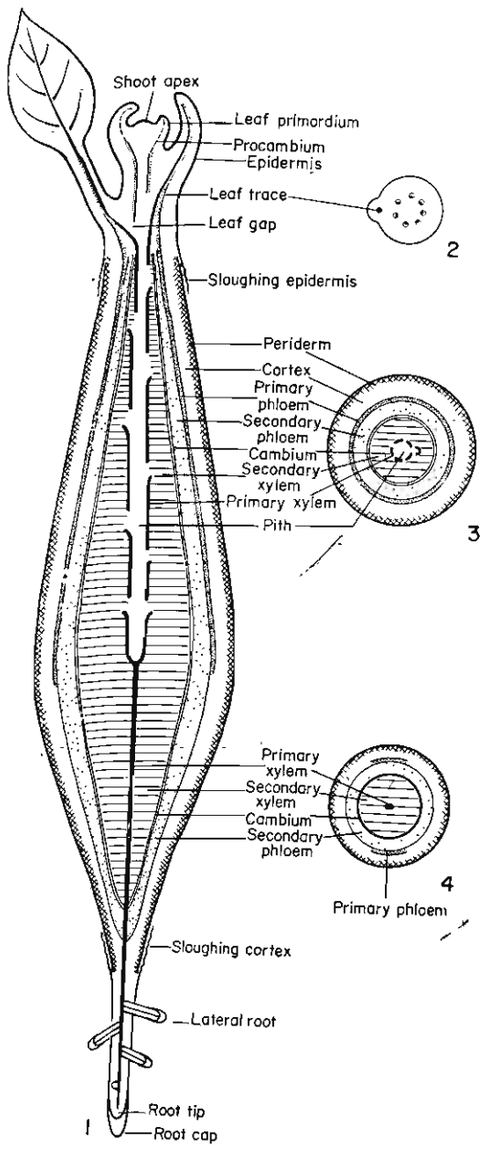

FIG. 3. Schematic drawings of a dicotyledonous plant showing the arrangement of the principal tissues. 1, Longitudinal section. 2, 3 and 4, Cross-sections at various levels. (Adapted from Esau, 1953.)

circumference inwards. In the root the direction of differentiation of the primary xylem is also centripetal, while in the stem these elements increase from the centre toward the circumference. Therefore in the stem the primary phloem and xylem approach one another during their development.

In monocotyledons and in a few herbaceous dicotyledons all the cells of the procambium differentiate into elements of the conductive tissues.

In most dicotyledons and gymnosperms, one layer of procambial cells between the primary xylem and primary phloem forms a new meristematic tissue called the *vascular cambium*. The vascular cambium produces secondary phloem towards the circumference, and secondary xylem towards the centre of the axis, as a result of cell division in a plane parallel to the circumference. The volume of the secondary tissues, especially of the xylem, continually increases and thus the thick stem and root of the shrub or tree is developed. In such a case the functions of the tissues produced by the apical meristems are restricted to the ends of the shoots and roots only. With the increase in width of the axis of the plant, as a result of the increase and development of the secondary vascular tissues, the epidermis and cortex peel off, and then the function of protection against external damage is taken over by a secondary protective tissue—the *periderm*. In the periderm a secondary meristematic tissue, the *phellogen*, is present. The phellogen produces the *phellem* (several layers of dead cork cells) towards the exterior and inwards, in the majority of cases, it produces the *phelloderm*, which consists of one to five layers of living cells.

The complex of plant tissues developing from the primary meristems, which are usually found in the apices of the roots and shoots, is termed the *primary plant body*, and those tissues developing from the vascular cambium and phellogen constitute the *secondary plant body*.

Leaves develop from the apical meristem. They consist of an *epidermis*, *mesophyll* and *veins*—strands of vascular tissue surrounded by parenchyma or by parenchyma and supporting tissues.

In addition to the tissues mentioned above, other tissues, such as *laticifers*, are found in the spermatophytes. Idioblasts, i.e. specialized cells, as well as some of the specialized tissues may develop from the basic tissues within the plant body.

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CHAPTER 2

THE CELL

THE basic units of which organisms are constructed are the cells. The term *cellula* was first used by Robert Hooke in 1665. Hooke gave this term to the small cavities surrounded by walls that he saw in cork; later he observed cells in other plant tissues and saw that they contained "juice" (Matzke, 1943).

Still later the *protoplasm*—the substance within the cell—was discovered. In 1880 Hanstein coined the term *protoplast* to indicate the unit of protoplasm found in a single cell. He also suggested that the term protoplast should be used instead of the term cell, but his suggestion is not generally accepted and cell is the accepted term. In plants the term cell includes the protoplast together with the wall.

The *cell wall* was, for a long time, regarded as a non-living excretion of the living cell matter, but recently more and more evidence has been found that organic unity exists between the protoplast and the wall, especially in young cells, and that the two together form a single biological unit.

In 1831 Robert Brown discovered the nucleus in an epidermal cell of an orchid plant. In 1846 Hugo von Mohl distinguished between the protoplasm and the cell sap, and in 1862 Kölliker introduced the term *cytoplasm*. From the end of the nineteenth century and during the twentieth century research on the cell has developed so rapidly and with such enormous strides that cytology has become a science of its own.

It is customary to divide the protoplast constituents into two groups: (a) *protoplasmic components* and (b) *non-protoplasmic components*.

To the first group belongs the *cytoplasm*, the "living" protoplasmic substance of the cell in which the specialized protoplasmic organelles, such as the nucleus and plastids, are located (Fig. 4, no. 6). The *nucleus* carries the information of heredity and so is of paramount importance to all the processes in the cell. The *plastids* usually contain pigments, but sometimes they are devoid of pigments and then they may store starch granules, lipid droplets and protein crystals. Other protoplasmic organelles are the *mitochondria*, which are minute bodies concerned in the respiratory processes and the *ribosomes*, still smaller organelles, which are the sites of protein synthesis.

To the second group belong the *vacuoles*, which are nonprotoplasmic inclusions surrounded by

include reserve materials such as starch grains, oil droplets, and aleurone grains, and other products of metabolism such as various crystals.

Usually the cell contains a single nucleus, but in some lower plants the presence of a nucleus with a distinct and permanent structure is doubtful.

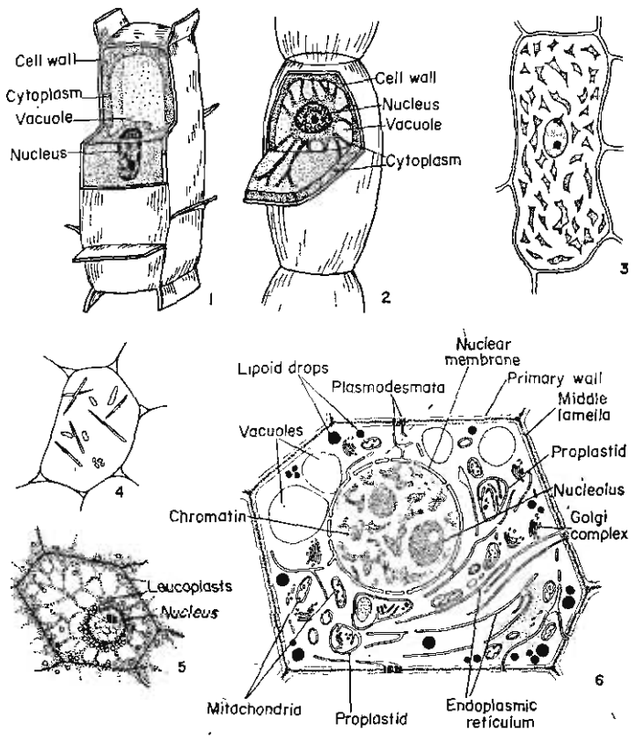

FIG. 4. 1, Three-dimensional diagram of a plant cell from which a portion has been removed to reveal a large central vacuole and the cytoplasm, which contains the nucleus, lining the cell wall. 2, As above, but of a cell in which the nucleus is located more or less centrally and in which the cytoplasm surrounding the nucleus is connected to the peripheral cytoplasm by cytoplasmic strands. 3, An adaxial epidermal cell from the calyx of *Tropaeolum majus* containing chromoplasts. 4, Chromoplasts in a carrot root cell. 5, Leucoplasts in a young endosperm cell of *Zea*. 6, Diagram of a meristematic plant cell. (No. 3, adapted from Strasburger, 1923; nos. 4 and 5, adapted from Eames and MacDaniels, 1947; no. 6, adapted from Sitte, 1961.)

In some cells of the higher plants, such as the sieve elements of the phloem which are adapted for translocation, the nucleus is absent from the mature cell. However, there are also cells which have numerous nuclei. A multi-

nucleated cell can comprise an entire organism as in some fungi and algae, or multi-nucleated cells may be a transitory stage in the development of a tissue as, for example, in the endosperm of many plants and sometimes in fibres. The accepted view in many cases is that each nucleus together with the protoplasm surrounding it forms a wall-less cell so that the entire multi-nucleate body comprises a group of protoplasmic units. Such a structure is called a *coenocyte*.

The coenocyte aroused much interest in phylogenetic and ontogenetic studies. Two theories exist which deal with the relation of the entire organism and the single cell. According to the *cell theory*, which was developed about the middle of the nineteenth century, the organism consists, both phylogenetically and ontogenetically, of a complex of an enormous number of cells each of which plays a role in determining the nature of the organism.

The theory contradicting the above is the *organismal theory*. This theory gives less importance to the individual cells and mainly stresses the unity of the protoplasmic mass of the entire organism. According to this theory the organism as a unit, to a large extent, determines the nature of the cells.

These two theories are important and, for the following reasons, attention was paid to both of them in histological and cytological research of plants. Many aspects of ontogeny, such as the processes of cell division, the origin of vessels and articulated laticifers, the development of idioblasts, etc., were investigated in the light of the cell theory. However, the specialization of the different cells and tissues in the plant and the sites of appearance of the various types of cells and tissues can be explained only on the basis of the organismal theory which regards the organism as an unit.

The protoplast

PROTOPLASMIC COMPONENTS

The cytoplasm

The cytoplasm comprises part of the protoplast. Physically it is a viscous substance which is more or less transparent in visible light. Chemically the structure of the cytoplasm is very complex even though the major component (85–90%) is water. Of the most important components of the cytoplasm are the proteins. Many of the physical properties of the cytoplasm can be explained by the fact that most of the inorganic and organic substances in it are present in colloidal solutions. However, these substances may occur in other states such as solutions and crystals.

Until recently the cytoplasm was considered to be structureless, but with the aid of the electron microscope it

covered within the cytoplasm. This structure, the so-called *endoplasmic reticulum*, consists of lipoproteinaceous membranes which form a capillary anastomosing system. Membranes of apparently similar structure are found on the external surface of the cytoplasm, i.e. the *plasmalemma* or *ectoplast*; on the border between the cytoplasm and the vacuoles, i.e. the *tonoplast*; and around the nucleus as well as around all the other protoplasmic organelles. The latter are themselves of membranous structure. There are indications that all the above membranes are interconnected. The lipids and proteins in these membranes are arranged in specific patterns which give the membranes special properties of permeability. The membranes are living parts of the cytoplasm and they alter according to the activity of the protoplast. The plasma membranes are especially characterized by their selective permeability to the passage of different substances through them.

The nucleus

The nucleus is a round or ellipsoid protoplasmic body (Fig. 5, no. 1). It is separated from the cytoplasm by the *nuclear membrane*. The nuclear membrane has been observed to consist of double porous lamellae (Fig. 4, no. 6). In many cases connections between these lamellae and the endoplasmic reticulum have been observed (De Robertis *et al.*, 1960). The nuclear sap or *karyolymph*, one or more *nucleoli*, and the *chromosomes* are found within the membrane. The chromosomes consist of *chromonemata*. The last two terms are derived from the word *chromatin* which means an intensely staining substance. The chromosomes consist of nucleoproteins of which the nucleic acid component is mainly DNA (deoxyribonucleic acid), the carrier of genetic information. Another group of nucleic acids is RNA (ribonucleic acid) which is concerned in the synthesis of proteins. Part of the RNA is formed on the DNA template. The prevailing nucleic acid in the cytoplasm is RNA.

The plastids

Various types of plastids can be distinguished. These differ from each other in structure and function, but develop from similar primordial organelles. One type of plastid may change into another. The classification of plastids is based on the presence or absence of pigments. Plastids lacking pigment are called *leucoplasts*, plastids with a green pigment, *chloroplasts*, and those with a pigment other than green, *chromoplasts*.

Leucoplasts are found in cells that have been protected from light and, in many cases, in mature epidermal cells (Fig. 58, no. 3). Leucoplasts are of varied and irregular shape. Usually the leucoplasts are concentrated

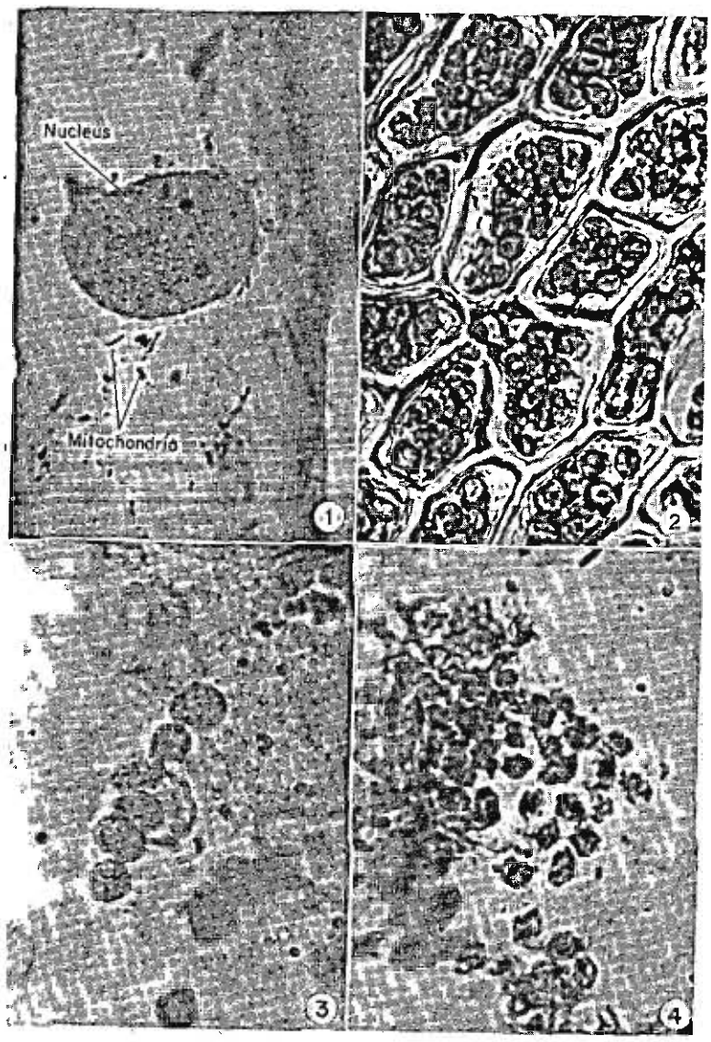

FIG. 5. 1, Portion of an epidermal cell of a bulb scale of *Allium cepa* showing the nucleus and mitochondria. ×830. 2, Cells of a moss leaf showing chloroplasts. ×740. 3, Chloroplasts in a subepidermal cell of the green fruit of *Lycopersicon esculentum;* grana can be distinguished as darker areas in the chloroplasts. ×660. 4, As above, but in a mature fruit where the chloroplasts have become changed into chromoplasts. ×660. (Nos. 3 and 4, courtesy of Y. Ben-Shaul.)

around the nucleus (Fig. 4, no. 5; Fig. 58, no. 3). Their main function is concerned with the development of starch grains. When the leucoplasts become specialized to store starch in those regions where starch is stored, they are called *amyloplasts*, and similarly those leucoplasts related to the

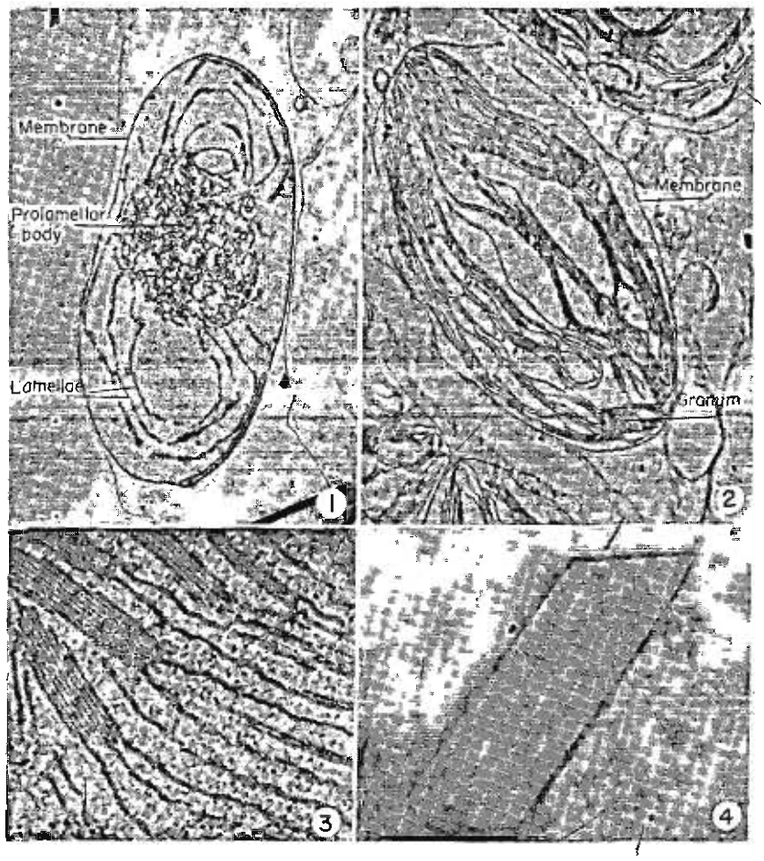

FIG. 6. Electron micrographs of plastids and their contents. 1, Proplastid of *Anacharis canadensis*. ×12,000. 2, Chloroplast of *A. canadensis*. ×10,000. 3, Grana in a chloroplast of *Zea mays*. ×95,500. 4, Carotene body from a carrot root. ×20,000. (Nos. 1 and 2, from Mühlethaler, 1960; no. 3, courtesy of S. Klein; no. 4, courtesy of Y. Ben-Shaul.)

production of oils and fats are termed *elaioplasts*. The latter are found mainly in liverworts and monocotyledons.

Chloroplasts contain all the enzymes responsible for photosynthesis and they are found in tissues exposed to light. They usually have the form of

flattened convex discs, plates or ellipsoids. Among the higher plants the average diameter of chloroplasts is 3 μ, but larger and smaller ones exist. The number of chloroplasts per cell depends on the particular tissue as well as the plant. In the higher plants there is always more than one plastid per cell (Fig. 5, no. 2). The chlorophylls (the green pigments) are aggregated within the plastid entirely, or almost so, in small bodies, the *grana* (Fig. 6, nos. 2, 3). The material in which the grana are dispersed is called the *stroma*. The protein content of the chloroplast is high. By means of the electron microscope a double-membrane envelope and an inner lamellar structure which is denser and more complicated in the grana was discerned.

Chromoplasts have various shapes which are usually irregular. They may be more or less round, elongated or angled and many of them are lobed (Fig. 4, nos. 3, 4). Their colour is variable—from yellow tones through orange to yellowish-red. The colour is due to *xanthophylls* and *carotenes*. The pigments are present in the chromoplasts in various forms—diffused, granular or crystalline. It is thought that it is the crystalline form that gives the various angular shapes to the chromoplasts as can be seen, for example, in the carrot root (Fig. 6, no. 4).

Chromoplasts play an important role in the composition of the colours of flowers and fruits, but they are also found in roots and other parts of plants. Many of them are chloroplasts that have undergone changes, but they can also develop directly from proplastids (Fig. 6, no. 1).

Development of the plastid

Plastids are found in large quantities in young meristematic cells where they are minute. At this primordial stage of development they are called *proplastids*. As the cell enlarges the proplastids reproduce and develop into mature plastids which are also able to reproduce but at a slower rate. The fact that one type of plastid may develop into another type is proof that all plastids have a common origin. For example, the chloroplasts of young fruits may develop into chromoplasts in the mature fruits, and the leucoplasts in the potato tuber become chloroplasts when exposed to light.

Mitochondria

The *mitochondria* are, as has already been mentioned, small protoplasmic organelles found in the cytoplasm. Mitochondria are thread- or rod-shaped (Fig. 5, no. 1). Their content is more dense than the cytoplasm and they consist mainly of proteins and lipids. From present data on the submicroscopic structure of the mitochondria it appears that the mitochondrion consists of two membranes: an outer limiting one and an inner one

which sends complex infoldings into the lumen of the mitochondrion. The lumen, which is surrounded by the inner membrane, is occupied by a relatively dense material, which is generally termed the mitochondrial matrix. Mitochondria are very sensitive to environmental influences and they are often destroyed by the usual fixation methods, especially those involving the acids, used in cytology and histology. Mitochondria are produced by division and are passed on from generation to generation via the gametes. Mitochondria contain enzymes that play a role in respiration.

Ribosomes and Golgi apparatus

The minute bodies that are often found connected to the endoplasmic reticulum are termed *ribosomes*. Their size is 100–200 Å. These bodies may be arranged in groups, are rich in RNA and were found to be centres of protein synthesis. In the cytoplasm there appear also special structures composed of double membranes and vesicles. These structures are known as *Golgi apparatus* or *Golgi complex*.

NONPROTOPLASMIC COMPONENTS

The vacuoles

Generally one or several vacuoles are present in the protoplast of plant cells. In many cells the vacuoles are so large that the cytoplasm forms an extremely thin layer which lines the cell wall and all the protoplasmic inclusions are localized within the cytoplasm on the circumference of the cell. Sometimes some cytoplasm is retained around the nucleus in the centre of the cell and cytoplasmic strands pass from it to the cytoplasm on the periphery of the cell (Fig. 4, nos. 1, 2). The vacuoles contain the *cell sap*. All the vacuoles, including the cell sap, of a single cell are termed the *vacuome*. The cell sap, which is not protoplasmic, consists of true aqueous or colloidal solutions. The substances that can be found in the cell sap are salts, sugars, polysaccharides such as inulin, organic acids, protein compounds, tannins, anthocyanins, flavones and others. These substances are ergastic and represent storage materials that can be utilized by the protoplast when necessary, or they are metabolic by-products. The tonoplast separates the vacuole from the cytoplasm.

Pigmentation

The plant pigments are usually found in the plastids and in the cell sap. The green colour is due to *chlorophyll* which is found in the chloroplasts. In the same plastids *carotenoids*, the yellow to orange pigments, are also

found but they are masked by the chlorophyll. *Carotenes* and *xanthophylls* belong to the carotenoids. The latter pigments become noticeable when there is little or no chlorophyll as is the case in the chromoplasts. Another group of pigments is the *flavones* which are water soluble and which colour the cell sap. In some genera, for example *Verbascum*, it is the flavones that give the yellow colour to the petals. The *anthocyanins*, which are the oxidation products of the flavones, are also water soluble and give red, purple, violet and blue colours to the cell sap. These pigments are responsible for the colouring of flowers, fruits, young leaves, etc. The colour of anthocyanins varies according to the pH of the cell sap: they are red in an acid medium and blue in a basic one. Sometimes the visible colour is the result of a few pigments occurring together in a single cell. For instance, chloro- or chromoplasts can be found together with anthocyanins.

White petals are devoid of pigments and the colour seen results from the reflection of light from the petals which are opaque due to the presence of numerous large intercellular spaces that are filled with air.

The colouring of autumn leaves is the result of various processes as well as the combination of different pigments. With the gradual death of the leaf the chlorophyll breaks down into colourless substances and the carotenoids become visible making the leaf appear yellow. The red and purple colours are from pigments in the cell sap, i.e. oxidation products of the flavones. These colours are most brilliant when formed in the presence of sugars in leaves exposed to strong light. Autumn colours, which result from the combination of small amounts of chlorophyll and carotenoids and greater amounts of anthocyanins together with tannins and various uncommon pigments and the browning of the cell wall, are best developed in the cold temperate zones.

Ergastic substances

Organic and inorganic by-products of metabolism such as mucilages, resins, gums, latex, tannins, alkaloids and others are found in the cytoplasm or in the vacuoles (Küster, 1956). Reserve food materials such as starch grains, aleurone grains, inulin (Fig. 7, no. 12) and oils may be present. Reserve food substances are found either in solution or as solid particles.

Starch. Starch grains are the most commonly found solid particles. They appear in different forms, but in the majority of cases they are spherical or egg-shaped (Fig. 7, nos. 1–11). When crowded, starch grains become angular. In some plants, as, for example, *Fagopyrum*, *Avena* and *Oryza*, the starch grains are compound. The size of starch grains varies greatly—their diameter in the potato tuber is from 70 to 100 μ; in *Triticum* caryopses from 30 to 40 μ; in *Zea* caryopses from 12 to 18 μ. In many plants it

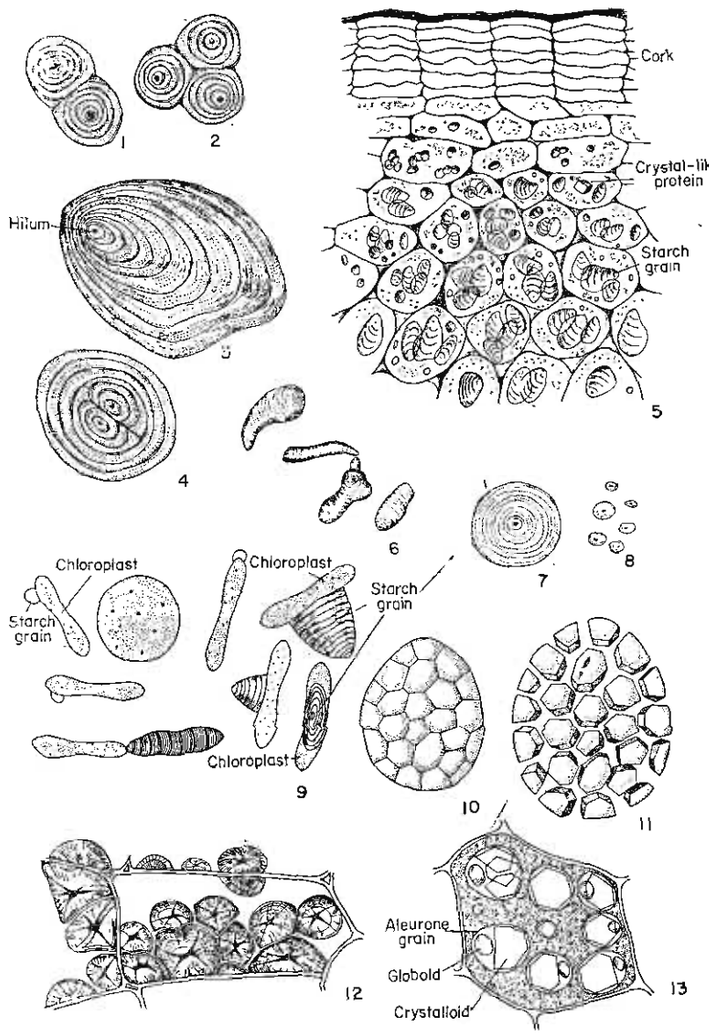

FIG. 7. 1–4, Potato starch grains. 1 and 2, Compound starch grains. 3, Simple starch grain. 4, Half-compound starch grain. 5, Cross-section of the outer portion of a potato tuber. 6, Banana starch grains. 7 and 8, Starch grains of *Triticum durum*. 9, Stages in development of starch grains in chloroplasts of *Phaius maculata*. 10, Compound starch grain of *Avena*. 11, As in No. 10, but disintegrating. 12, Sphaerocrystals of inulin in cells of a *Dahlia* tuber. 13, Aleurone grains in an endosperm cell of *Ricinus communis* from a section of material embedded in dilute glycerine. (Most of the figures adapted from Strasburger, Palladin and Troll.)

is possible to distinguish concentric layering in the starch grain. These layers are laid down successively around the *hilum*. In compound grains several such hila are present. The successive layers differ in their density and water content. Starch, when organized in grains, is optically anisotropic. This fact can be observed when the grains are examined under polarized light.

Starch develops within the plastids. The *assimilation starch*, a temporary product of photosynthesis, is formed in the chloroplasts (Fig. 7, no. 9). *Storage starch* is formed in leucoplasts. One or more starch grains may be formed in a single plastid. As the grain enlarges the plastid swells and its contents usually are displaced to one side of the grain, so that most of the grain is covered by a very thin layer of plastid material.

Proteins. Ergastic protein is reserve material in amorphous or crystal-like form. Amorphous protein is found together with starch in the endosperm of wheat grains. Crystal-like protein, in the form of small cubes, is found in the parenchyma cells of the outermost regions of the potato tuber. Crystal-like and amorphous protein are found together in aleurone grains in the endosperm and embryo of many seeds (Fig. 7, no. 13).

The development of *aleurone grains* in the seed of *Ricinus* has been described in detail by Frey-Wyssling (1948). The aleurone grains are formed from readily soluble proteins with globular molecules and relatively low molecular weight which accumulate in the vacuoles of the storage cells where they crystallize. From these liquid vacuoles water is lost. This causes the various vacuolar components to precipitate according to their solubility. In *Ricinus* the first substance to be precipitated is the almost insoluble phytin (magnesium–potassium salt of inositol phosphoric acid); this substance forms the globoid. Next, the corpuscularly dispersed reserve proteins precipitate out in a lattice to fill the remaining space of the vacuole and so form the crystalloid part of the aleurone grain. Finally, the remaining liquid, which now contains soluble albumin, solidifies to form a homogeneous substance which surrounds both the globoid and crystalloid.

Fatty substances. Oils and fats (storage lipids) and other compounds with lipid characteristics, such as waxes, suberin and cutin, are also ergastic substances. These substances are formed directly by the cytoplasm and the elaioplasts. Oils and fats are common reserve materials in seeds, embryos and meristematic cells. The essential oils also belong to this group. In certain plants, such as the conifers, essential oils are found throughout the plant, but in other plants they are found only in the leaves, petals or peels of fruits.

Crystals. As was mentioned previously, crystals are the by-products of the metabolic processes of the cell. These crystals are of differing chemical composition and are found in many kinds of cells of the plant. The most common crystals are those of calcium salts, especially calcium oxalate. Crystals of inorganic compounds, such as gypsum and silica, are less

common. Crystals of organic substances, such as carotene, berberine and saponin, are relatively common. The shape of crystals in plants varies very greatly (Fig. 8, nos. 1–3). They may be solitary, rhomboidal, octahedral, or very much elongated. The elongated crystals, when massive and occurring solitarily, as for example in the Iridaceae, are called *styloids*, and when thin and occurring in bundles, *raphides*. Crystals may be compound and clustered in spherical masses and then they are termed *druses*. Small prismatic crystals as well as minute crystals, called *crystal-sand*, are also common.

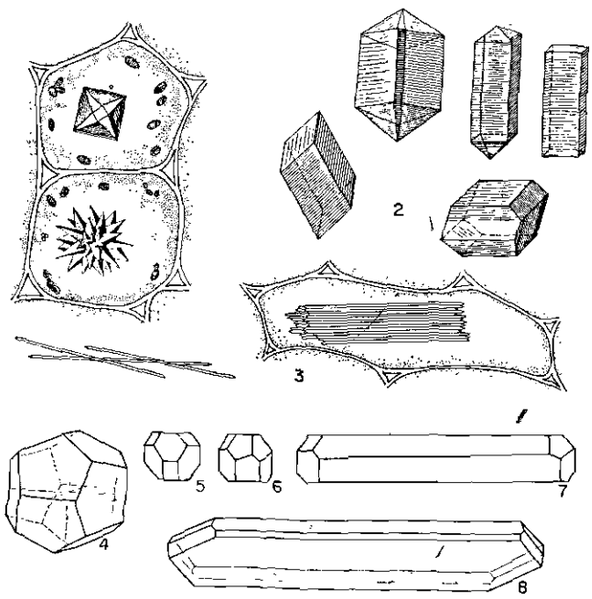

FIG. 8. 1, Two parenchyma cells from the petiole of *Begonia;* in the upper cell a solitary prismatic crystal and in the lower cell, a druse. 2, Variously shaped prismatic crystals. 3, Individual raphides and a bundle of raphides. 4, A cell with pentagonal faces. 5–8, Various types of cell shapes with 14 faces. (Nos. 1–3, adapted from Palladin, 1914; nos. 4–8, adapted from Frey-Wyssling, 1959.)

Crystals of calcium oxalate are found usually in the vacuole but some workers (for instance, Scott, 1941) refer to crystals that develop in the cytoplasm. Crystals can be found in cells resembling those neighbouring them but lacking crystals, or they may be confined to special crystal-containing cells, i.e. *idioblasts* (Foster, 1956).

Idioblasts are cells that differ distinctly from the surrounding cells in both shape and structure. Raphides are usually found in very large cells which, when mature, do not contain a living protoplast, but which are

filled with mucilage. Idioblasts with raphides are found in many monocotyledons and also in some dicotyledons as, for instance, in the petals of *Impatiens balsamina.*

Silicon salts are often deposited in cell walls, as is common in the grasses, but they can also be found within the cell.

Cystoliths. These are internal outgrowths of the cell wall that are encrusted with calcium carbonate (Fig. 55, no. 1).

Tannins. The tannins are a heterogeneous group of phenol derivatives. In microscopical sections of tissues tannins are usually identifiable in the cells as yellow, red or brown substances. Tannins can be found in the different parts of the plant, especially leaves, the periderm, galls, and in cells associated with vascular bundles. Tannin-containing cells may be interconnected or tannins may be found in isolated specialized cells (idioblasts). Within the cell the tannins may be found in the vacuole or in the form of droplets in the cytoplasm, and sometimes they penetrate into the cell wall, as, for instance, in cork tissue. Tannins are thought to protect the plant against dehydration, rotting and damage by animals.

The cell as a tissue component

Mature cells vary in size and shape. Cells may be ellipsoidal, ovate, cylindrical, flattened, prism-like, star-shaped, fibre-like, and lobed. Parenchyma cells are usually from 10 to 100 μ in diameter, but in fleshy fruits and the pith of stems larger cells can be found. Fibres are usually about 1–8 mm long but fibres 55 cm long are also known, e.g. in *Boehmeria.*

BASIC SHAPE AND ARRANGEMENT OF CELLS

As the cell volume increases in the meristematic region the primary elastic cell wall tends to assume the smallest possible surface area, i.e. the form of a sphere. After mitosis, forces act that tend to impart to the cell a spherical form, but as there are no intercellular spaces in the meristem, the cells, which are densely arranged, become polyhedral in shape (Fig. 8, no. 4). The basic shape of cells is a 14-faced polyhedron (Matzke, 1946). However, in plant tissues, cells with 12, 13, 15, 16 or more faces are found. Most of the faces of the cell wall are, according to Matzke, pentagonal (Fig. 8, no. 4) but tetragonal and hexagonal faces can also be found (Fig. 8, nos. 5–8). Similar structure was found in bubbles of soap foam, and also in experiments where lead shot was subjected to sufficient pressure to cause the elimination of the air spaces (Marvin, 1939).

Accordingly, the basic shape of the cells of the apical meristems is of a 14-faced polyhedron (Fig. 8, no. 4) in which most of the faces are penta-

gonal and the remaining ones tetra- or hexagonal. In the apical meristem of *Anacharis densa*, Matzke (1956) found that during the interphase the average number of faces of the polyhedron increased from 13·85 to 16·84, and after division the daughter cells had an average of 12·61 faces.

As result of the continued increase of cell volume during growth, the number of wall faces increases above 14. This makes it impossible for all the sides to remain in contact with all the sides of the neighbouring cells and so *intercellular spaces* develop. In some tissues the intercellular spaces reach relatively large dimensions and then they are referred to as *air spaces*, *ducts*, etc. Such spaces can develop in two ways: (a) by the separation of neighbouring cell walls, as in the development of the resin ducts in *Pinus*; this type of development is known as *schizogenous* development (Fig. 33, nos. 2–5); (b) by the disintegration of the cells in the place where the space develops, as in the essential oil cavities in the peel of citrus fruits; this type of development is known as *lysigenous* development (Fig. 34, nos. 1–6). In some cases spaces are formed by these two methods together and then the development is known as *schizo-lysigenous* development. The intercellular spaces in the protoxylem are sometimes formed in this way.

The intercellular spaces can be irregular and variable in shape or they may form a distinct and permanent system as in many water plants, in the banana leaf, and other plants (Fig. 93, no. 3; Fig. 97, no. 1).

INTER-RELATIONSHIP OF CELLS DURING GROWTH

All cells develop from existing cells by cell division. The young cells in the growing regions are all relatively small; as they mature their size and shape alter in accordance with their physiological function. As the cell wall is already present at the earliest stages of development of the cell it takes part, together with the protoplast, in the processes of cell growth.

When a group of cells grows together uniformly, the cells of the group take up different positions and shapes, but the relationships between the neighbouring cell walls do not change and no new areas of contact are formed between the cells; this type of growth is known as *symplastic growth*. In many cases growth results in the alteration of the existing relationships between the cell and in development of new contacts between neighbouring cells; such processes take place in *gliding* and *intrusive growth*. In gliding growth the cell wall of one cell slides over that of the neighbouring cell thus forming new areas of contact both between cells that were already in contact and between cells that were not previously in contact. This type of growth is found during the production of new initial cells in a non-storied cambium, and during the development of xylem and phloem elements. Intrusive growth is that growth in which portions of cells continue to grow, and in doing so penetrate between neighbouring cells with which

new areas of contact are formed. In such cases there is no gliding. In many plants the ends of the fibres grow in this way. The growth of the branches of some sclereids and of the non-articulated laticifers is intrusive.

Many cells whose growth continues over a long period develop by all three methods of growth, or by two of them.

The cell wall

The presence of a wall in plant cells distinguishes them from animal cells. Among the vascular plants only certain cells, connected with the reproductive processes, are naked; all other cells have walls.

The cell wall was discovered in the seventeenth century before the presence of the protoplast was recognized and since then many researchers have investigated the cell wall. Various methods—chemical, physical and morphological—have been used. These investigations were assisted by advances in organic chemistry, X-rays, the use of the light and polarizing microscopes, and, recently, by the electron microscope.

NATURE OF THE CELL WALL

Contrary theories exist as to the nature of the wall. According to one theory the cell wall, at least during its growth, contains protoplasmic material. According to another theory the cell wall is a dead excretion on the surface of the protoplast. According to both theories however, the cell wall grows when in contact with the protoplast but outside of it. Only in the spores of some pteridophytes does the outer part of the wall develop from the tapetum which surrounds the spores while they are being formed (Sharp, 1943).

FORMATION OF THE WALL

During mitosis, at the telophase, the phragmoplast widens and becomes barrel-shaped. At the same time, on the equatorial plane the *cell plate*, i.e. the first-evident partition between the new protoplasts, begins to form inside the phragmoplast. In the area where the cell plate forms, the fibres of the phragmoplast become indistinct and are restricted to the circumference of the cell plate (Fig. 9, nos. 3–5). With the enlargement of the cell plate the fibres of the phragmoplast approach the wall of the dividing cell. In very long cells, such as the fusiform cells of the cambium, the cell plate soon reaches the side walls of the dividing mother cell, but contact with the end walls of the cells is delayed and thus it is possible to see the fibres of the phragmoplast arranged in two lines perpendicular to the longitudinal

axis of the cell (Fig. 124, nos. 3, 4). In such cells the young nuclei almost reach the resting state, with a membrane and nucleoli, while the cell plate has not yet reached the end walls of the dividing cell. When the cell plate reaches all parts of the existing wall of the dividing cell the phragmoplast disappears completely. At this stage the viscosity of the cell plate becomes

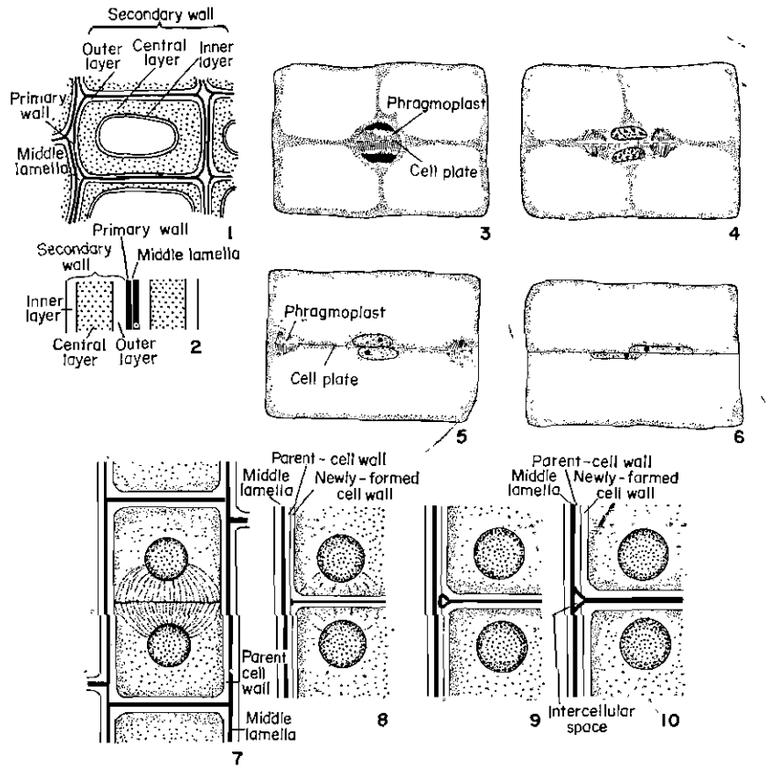

FIG. 9. 1 and 2, Diagrammatic sections of cells with secondary walls. 1, Cross-section. 2, Longitudinal section. 3–6, Stages in cell division showing the development and growth of the cell plate. 7–10, Schematic drawings showing the connection of the newly formed wall to the wall of the cell that underwent division. (Nos. 1 and 2, adapted from Kerr and Bailey, 1934; nos. 3–6, adapted from Sinnott and Bloch, 1941; nos. 7–10, adapted from Martens, 1937.)

higher, and on both sides thin lamellae are laid down by the daughter protoplasts. These lamellae are the initial stage in the development of the new walls of the daughter cells. The cell plate gradually undergoes changes to form the intercellular substance referred to as the *middle lamella.* It is not yet known what substance comprises the cell plate; it is possible that it is of protoplasmic origin.

Along the line of contact of the new wall and the wall of the mother cell, the new and old middle lamellae are separated by the primary wall of the mother cell (Fig. 9, no. 8). According to Martens (1937, 1938) the connection between these middle lamellae is effected in the following manner. In the primary wall of the mother cell a cavity, which is triangular in cross-section, develops all along the line of contact of the new and old walls. This cavity continues to enlarge till it reaches the middle lamella of the mother cell and so connection is made between the new and old middle lamellae. If the cavity continues to grow and the intercellular substance does not fill it, an intercellular space lined with intercellular substance is formed. According to Priestley and Scott (1939) the middle lamellae are brought into contact after the stretching wall of the mother cell tears opposite the new wall.

COMPOSITION AND GROSS STRUCTURE OF THE WALL

On the basis of the development and structure of plant tissues it is possible to distinguish the following principal three layers in the cell wall: (a) the *middle lamella* or the *intercellular substance*; (b) the *primary wall*; (c) the *secondary wall* (Fig. 9, nos. 1, 2). The middle lamella is the cement that holds the individual cells together to form the tissues and, accordingly, it is found between the primary cell walls of neighbouring cells. The secondary wall develops on the inner surface of the primary wall.

The *middle lamella* consists of colloidal matter that is optically inactive (isotropic). The basic constituents of the middle lamella are calcium and magnesium pectates. In addition to these substances protein substances are apparently also present.

The *primary wall* is the first true cell wall, which develops on the new cell, and in many cells it is the only cell wall, as the middle lamella is regarded as intercellular substance and not a wall proper. The primary wall is that part of the cell wall that develops in cells or portions of them which are still growing. This wall is optically active (anisotropic), and it contains cellulose, pectic compounds as well as hemicellulose and polysaccharides other than cellulose.

The *secondary wall* is formed on the inner surface of the primary wall. It begins to develop in cells or parts of them that have ceased to grow. The secondary wall consists of cellulose and other polysaccharides including hemicellulose. In addition to these substances deposits of lignin, suberin, cutin, waxes, tannins, inorganic salts, such as calcium carbonate and calcium oxalate, silica and other substances may occur in the secondary walls. The lignin first appears in the intercellular substance and primary wall from where it spreads centripetally through the secondary wall as this wall develops.

The secondary wall is very strongly anisotropic and layering can be observed in it. The reason for this layering is discussed later in this chapter. In the majority of tracheids and fibres three layers—the *outer layer* (S_1), *central layer* (S_2), and *inner layer* (S_3)—can be discerned in the secondary wall. Of these layers the central layer is usually the thickest. In some cells, however, the number of layers may be more than three (Fig. 10, no. 1).

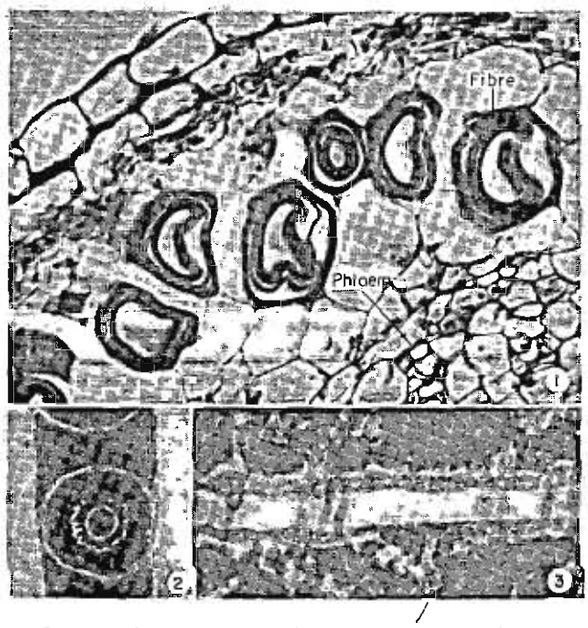

FIG. 10. 1, Outer portion of a cross-section of a young stem of *Linum usitatissimum* showing maturing fibres in which the various layers of the secondary wall have separated from each other during sectioning. ×460. 2, A dark-field photograph of a bordered pit of *Cedrus* showing the fringed torus. ×700. 3, Electron micrograph of a cross-section of a pit membrane of a living fibre of *Tamarix* showing plasmodesmata. ×35,000. (No. 2, from Huber in *Handbuch der Mikroskopie in der Technik*, Umschau Verlag, 1951.)

Some authors (for example, Meier, 1957) use the term tertiary wall or tertiary layer for the inner layer of the secondary wall. According to Frey-Wyssling (1959) an innermost layer with a chemical composition different from that of the secondary wall may be present in addition to the inner layer of the secondary wall. He suggests that this layer should be called the *tertiary* or *terminal layer*.

It should be mentioned that some investigators use the term *compound middle lamella* when dealing with wood tissue. This term is used to refer

to the complexes of lignified layers which appear more or less homogeneous when examined under the light microscope with no pretreatment. The compound middle lamella may be three-layered and then it refers to the middle lamella proper and the adjoining primary walls, or five-layered, and then it refers to the middle lamella proper, the primary walls and the outer layer of the secondary walls of the adjoining cells (cf. Kerr and Bailey, 1934).

FINE STRUCTURE OF THE CELL WALL

The fine structure of the cell wall, particularly that of the secondary wall, has been intensively studied in the last century. This research was stimulated because of its importance to the fibre, paper and other industries. The researchers worked in two directions, i.e. from the morphological and physico-chemical approaches. By combining the results of these two fields of research a rather clear picture of the fine structure of the cell wall has been derived.

Results of the morphological line of research. With the high power magnification of the ordinary light microscope, different arrangements of the layering in the secondary wall can be seen in cross-sections of fibres, tracheids, hairs, etc. The layers can be concentric, radial or have a complicated arrangement. When the cell wall is allowed to swell under the influence of suitable reagents, fine structures can be observed with the aid of the light microscope (Fig. 11, no. 1). By means of such methods Bailey and others (Bailey and Kerr, 1935; Bailey and Vestal, 1937 a, b; Bailey, 1957) found that the cell wall is built of a system of microscopic threads—the *microfibrils*, which are grouped together in larger bundles. The layering seen in the secondary wall is often the result of the different density of the microfibrils; this is the case in cotton fibres, for example. In the denser, darker wall layers, the microfibrils are more numerous per unit area and they are more tightly packed. In the less dense, lighter wall layers, the microfibrils are looser and the capillary spaces between the fibrils are larger. In heavily lignified walls it is possible to dissolve the cellulose and retain the lignin only, or the lignin alone can be dissolved and the cellulose retained. In this way the component retained gives, as it were, a negative image of the component which has been dissolved. This phenomenon not only proves that the lignin is found in the elongated interfibrillar spaces of the cellulose but also that these capillary spaces are continuous. Therefore it is clear that the secondary wall consists of two continuous interpenetrating systems, one of which is the cellulose microfibrils, and the other the continuous system of microcapillary spaces. These spaces may be filled with lignin, cutin, suberin, hemicelluloses, and other organic substances and even mineral crystals, and in fresh tissue aqueous solutions. The

material between the microfibrils forms the noncellulosic matrix. Not all the layering of the secondary wall that can be seen with the light microscope is the result of the degree of density of the cellulosic microfibrils as was suggested previously. In tracheary elements and sclerenchyma cells the more pronounced layers are usually the result of the different quantities of lignin, pectic substances, hemicellulose or other organic substances de-

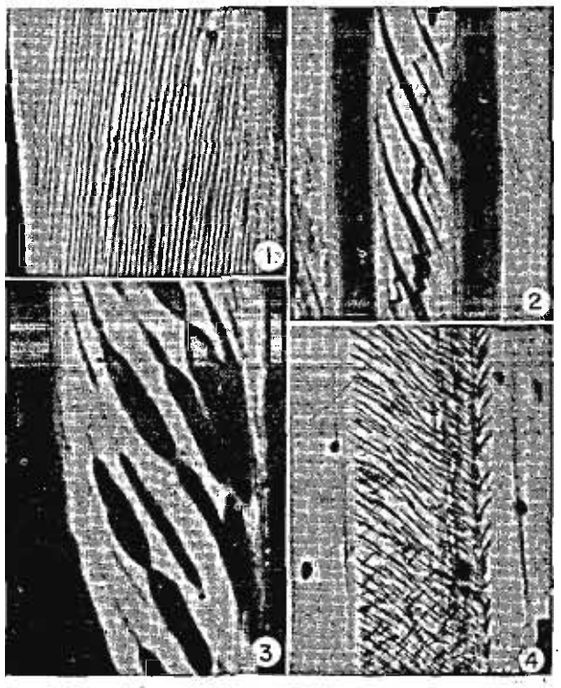

FIG. 11. 1, Striations seen on the surface of a tangential section of the secondary wall of a fibre-tracheid of *Siparuna bifida*. ×1100. 2, A longitudinal section through the secondary wall of a tracheid of *Pinus* showing the plane of mechanical cleavage. ×460. 3, A longitudinal section in the secondary xylem of *Pinus* showing the spiral arrangement of the cavities produced by enzymatic action of fungi on the secondary wall. ×230. 4, Longitudinal section of tracheids of *Larix* showing the orientation of iodine crystallized in the spaces between the microfibrils. ×480. (Courtesy of I.W. Bailey.)

posited in the interfibrillar spaces of the cellulose, or of the presence, in certain cells, of layers lacking cellulose, or of the different orientation of the microfibrils in the various wall layers.

In order to demonstrate the presence of the two parallel, three-dimensional systems, the cellulosic microfibrillar network and the network of

interfibrillar microcapillary spaces, Bailey used methods other than those described above. For example, he succeeded in crystallizing iodine in the elongated, microcapillary spaces (Fig. 11, no. 4) thus demonstrating their presence and the orientation of the microfibrils in the different layers of the wall.

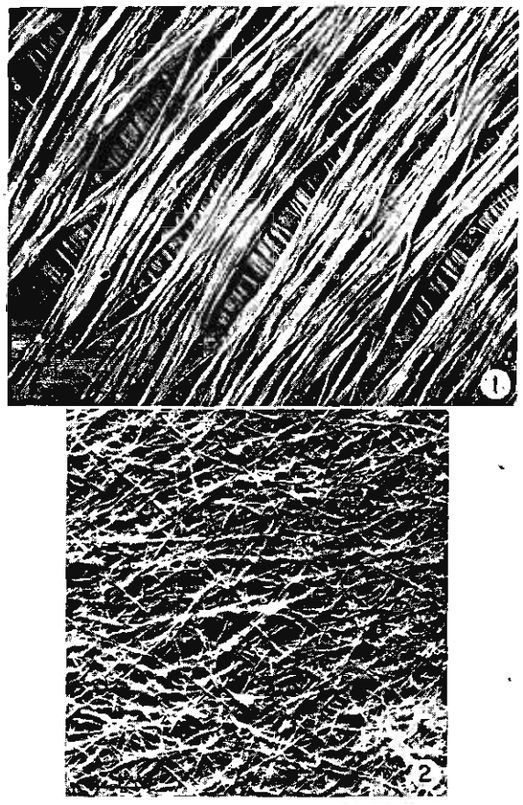

FIG. 12. 1, Electron micrograph showing the structure of the secondary wall of *Valonia*. ×7000. 2, As above, but of the primary wall. ×8000. (From Steward and Mühlethaler, 1953.)

The second stage in the morphological research of the fine structure of the cell wall is based on the use of the electron microscope. Among the outstanding research workers of this stage are Frey-Wyssling, Mühlethaler, Roelofsen, Preston and Wardrop.

Although there are many restrictions, mainly because of the methods of preparation of the material to be examined, the electron microscope has

made possible many advances in the study of the structure of the cell wall. The amazing photographs which were made with the electron microscope (Fig. 12, nos. 1, 2) revealed the fine microfibrils which cannot be seen by means of the ordinary light microscope. The results of research with the electron microscope have in general confirmed the theories of Bailey on the structure of the wall.

The morphological structure of the cellulose in the cell wall, as is known today, can be summarized in the following way. Within the cell wall differently arranged lamellae are recognized, each of which consists of microfibrils. According to at least some researchers the microfibrils are grouped in bundles. These bundles as well as the microfibrils anastomose to form a three-dimensional network. This network is interwoven with a parallel network of microcapillary spaces occupied by noncellulotic substances.

The width of the microfibrillar bundles can be as much as 0·25 μ, and that of the microfibrils themselves, as measured from fibres of *Boehmeria*, 0·02μ (170–200 Å) approximately. However, thinner and sometimes even thicker microfibrils are found in different cells and plants. The microfibrils have recently been found to be fasciations of *elementary fibrils* which are about 35 Å thick.

Results of the physico-chemical line of research. The cellulose molecule consists of long chains of linked glucose residues. The chain molecules are arranged in bundles which are generally termed *micellae*. The hypothesis of the presence of micellae was proposed by Nägeli in the last century. According to him the micellae are the individual units arranged in a permanent order within an intermicellar matrix. With the aid of the polarizing microscope the crystal-like nature of the micellae was proven. From the results of various investigations, especially those made with X-rays, investigators came to the conclusion that the micellae consist of parallel chains of glucose residues which have characteristic and permanent distances between them. As a result of extensive research carried out in the last thirty years by botanists, chemists and physicists, several theories were suggested which attempted to explain the organization of the cellulose molecules in the cell wall. Frey-Wyssling and Mühlethaler have recently come to the following conclusion as regards the structure of cellulose. The thread-like cellulose molecules are regularly arranged in bundles. Each such bundle, which forms an elementary fibril, consists of about 36 cellulose molecules. The elementary fibril is in greatest part crystalline. Only very small parts of it, which are presumably arranged at random, may be paracrystalline. The number of glucose residues in cellulose molecules of fibre cells was found to vary from 500 to 10,000 and the length of these molecules varies from 2500 to 50,000 Å (Frey-Wyssling, A. and K. Mühlethaler, 1965. *Ultrastructural Plant Cytology*. Elsevier Publishing Co.) (Fig. 13).

Most of the above is based on the results of research made on the secondary cell wall, but recently much attention has been paid to the structure of the

primary wall. The primary wall is similar in structure to the secondary wall in that it consists of anisotropic (crystalline) cellulose microfibrils and a noncellulotic matrix. Sometimes, as in the Phycomycetes, the microfibrils consist of chitin (Frey-Wyssling and Mühlethaler, 1950; Roelofsen, 1951)

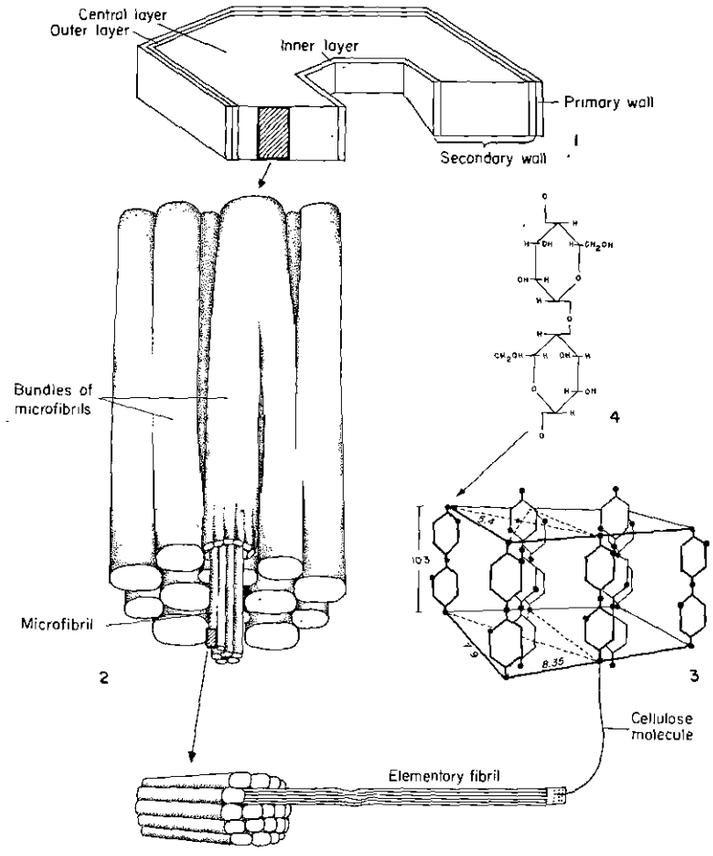

FIG. 13. Diagrammatic representation of the submicroscopic structure of the cell wall. 1, Portion of a cell with secondary wall layers. 2, Bundles of microfibrils, microfibrils and an elementary fibril. 3, Two unit cells of cellulose, as suggested by Meyer and Mark. 4, Two glucose residues.

or of other substances. The interfibrillar matrix usually contains pectic compounds and hemicellulose, but in many cells lignin, cutin, suberin, waxes and many other organic substances may also be present. The primary wall of many cells has a lamellate structure. The

microfibrils cross in the primary wall differs in different cells as well as in the various lamellae and in different parts of the wall of a single cell (Fig. 12, no. 2).

New theories, based on electron microscopic research, have been developed as to the manner in which the primary wall grows (Wardrop, 1962). Frey-Wyssling and Stecher (1951), for instance, suggested that the primary cell wall grows in a way that has been termed *mosaic growth*. In such growth thin areas, penetrated by the cytoplasm, appear in the growing primary wall. In these regions cytoplasmic synthesis takes place so that the microfibrils are pushed apart by the enlarging mass of cytoplasm, thus enlarging the cell surface. Subsequently new microfibrils are woven into the wall to fill in the thinner areas. A more recent concept is the theory of *multinet growth* (Houwink and Roelofsen, 1954). According to this theory the thickening and increase in surface area of the primary wall is brought about, in many cases, by the separation of the crossed microfibrils and alteration in their orientation, in the earliest formed lamellae, from being almost transverse to almost longitudinal. New lamellae with denser, crossed and almost transversely orientated microfibrils are added centripetally.

The classical debate as to whether the growth of the cell wall is accomplished by *intussusception* or by *apposition* is, therefore, still continued. According to the first opinion the material of the new wall is laid down between particles of the existing substance of the expanding wall. According to the second opinion the growth is due to the centripetal addition of new layers, one upon the other. However, in the light of present knowledge it appears that the theory of apposition is the more acceptable.

ORIENTATION OF MICROFIBRILS, MICELLAE AND CELLULOSE CHAINS

In order to discover the orientation of the microfibrils, the micellae and the cellulose chains in the different layers of the cell wall, and particularly in the secondary wall, many investigations have been made (Bailey and Kerr, 1935, 1937; Bailey and Vestal, 1937a, b; Bailey and Berkley, 1942; Wardrop and Preston, 1947; Frey-Wyssling *et al.*, 1948; Frey-Wyssling, 1948, 1950; Bailey, 1957; Wardrop, 1954, 1958; and others). These investigations were based on all of the methods, both direct and indirect, that were described previously. In general, the results obtained by different methods of investigation on the same object have proved similar. The orientation of the microfibrils and of the bundles of microfibrils in two layers can be determined simultaneously in specially prepared sections (Fig. 12, no. 1). The orientation of iodine crystals in the interfibrillar spaces can also be seen easily with high magnification of the ordinary light microscope. Electron micrographs are also of value where the axes of the cells can be marked on the small portion of the wall seen in them.

When a thin cross-section through tracheids is examined with a polarizing microscope while the two Nicol prisms are crossed, certain layers of the wall appear bright and others dark (Fig. 14, nos. 2, 4, 5). In the brightest layers, those with the strongest birefringence, the longitudinal axes of

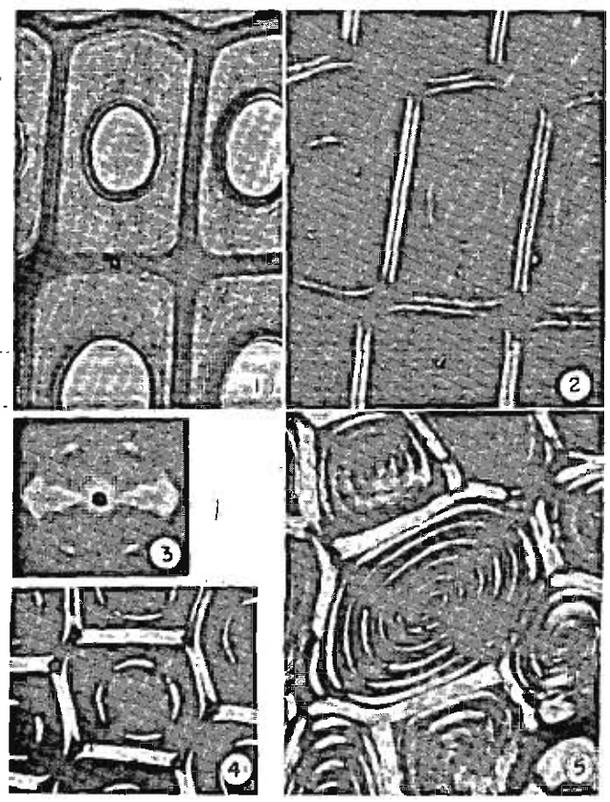

FIG. 14. 1, Micrograph of a cross-section of tracheids of *Pinus* in which three layers can be distinguished in the secondary wall. 2, As above, but as seen under the polarizing microscope. 3, X-ray diffraction pattern of delignified wood of *Pinus longifolia*. 4, As in No. 3, but as seen in a polarizing microscope. 5, Micrograph of a cross-section of fibres of *Pandanus* as seen in the polarizing microscope showing the numerous concentric layers in the secondary cell wall. (Courtesy of I.W. Bailey.)

the crystals of cellulose are parallel to the surface of the section, i.e. perpendicular to the longitudinal axis of the tracheid. In the layers in which the cellulose crystals are perpendicular to the surface of the section the passage of light is not affected and the layers remain dark between crossed

prisms. In these layers the crystals are parallel to the longitudinal axes of the tracheids. The bright layers, however, are not continuous on the circumference but are interrupted in four places. The brightest sections of such a layer are those that lie at an angle of 45° to the axis of the analyser and the polarizer of the microscope, and the darkest areas of the same layer are approximately parallel to these axes. The birefringence is only apparent

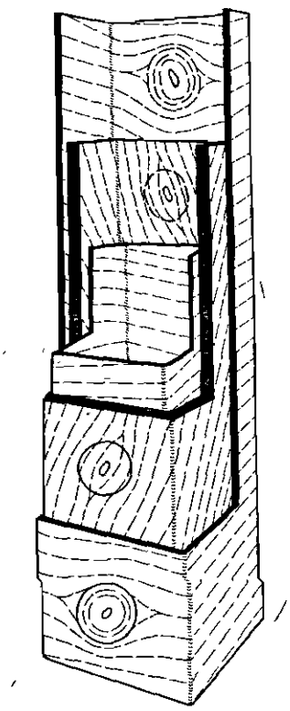

FIG. 15. Three-dimensional schematic drawing of a tracheid to show various secondary wall layers and the orientation of the microfibrils in them and around the bordered pits. Microfibrils indicated by broken lines. (Adapted from Brown *et al.*, 1949.)

when the longitudinal axes of the crystals are at an angle of 45° to the axes of the crossed analyser and polarizer. By the study of oblique sections, cut at different angles or on the basis of accurate calculations of the degree of the birefringence, it is possible to use this method to determine the accurate orientation of the cellulose crystals in the various layers of the wall (Preston, 1952).

From the results obtained from investigations using X-rays, the orientation of the cellulose crystals in the different layers cannot be determined

only conclusions as to the average orientation of the different wall layers of a large number of cells can be drawn. In order to make X-ray photographs, sections of tissue about 1 mm thick are used. The angle between the longitudinal axis of the cellulose crystals and that of the cell is calculated according to size of the preferred orientation of X-ray diffraction spots (Fig. 14, no. 3).

From the results of the above investigations, it is seen that the orientation of the microfibrils and the micellae in the secondary walls differs in different plants, in the cells of the different plant organs, in the different layers of the same cell wall, and sometimes even in the different lamellae of the same layer. In the walls of many vessel members, tracheids and fibres that have been studied and that have three layers to the secondary wall, the following arrangement of the microfibrils and micellae has been found: the orientation in the outer and inner layers is almost horizontal or the microfibrils are orientated in a very low spiral; and the orientation in the central layer is almost parallel to the longitudinal axis of the cell, the microfibrils being arranged in a steep spiral (Fig. 15).

Bailey and Vestal (1937a) found that in the outer wall layer of the tracheids of early conifer wood the orientation of the cellulose microfibrils around the large bordered pits is circular, while the microfibrils in the central layer are only slightly deflected around the pits.

In cotton fibres the largest portion of the secondary wall consists of spirally arranged microfibrils that are orientated at an angle of 45° or less to the longitudinal axis of the cell. In flax fibres the orientation of the microfibrils is spiral, but the direction of the spiral in each of the numerous overlying layers opposes that in the adjacent layers.

PROPERTIES OF THE WALL RELATED TO ITS STRUCTURE

As has been mentioned previously, the wall in a cross-section appears to be built of layers, because of the different composition and structure of the lamellae which are added continuously as the wall grows. The difference in the structure is brought about, as explained above, by the differences in density and orientation of the cellulose microfibrils, the presence of different quantities of lignin, etc. These features result in differences in the refraction of light so that the layers of the wall are emphasized.

Because of the large amount of cellulose in the wall, the properties of the wall are determined by those of cellulose; the other substances add some characteristics, or alter slightly, those of the cellulose. One of the important properties of cellulose is its ability to withstand stretching because of its elasticity. The lignin increases the resistance of the wall to pressure and so prevents the folding of the cellulose microfibrils. The orientation of the microfibrils in the different lamellae of the wall no doubt is an important factor in determining the

SPECIAL STRUCTURES OF CELL WALLS

Primary pit fields

The primary walls of young cells stretch and increase in surface area and thickness as the cell grows. However, certain portions of the wall generally remain thin; these portions are termed *primary pit fields* (Fig. 16, nos. 1, 2). Sometimes, when the pit fields are numerous and deeply sunken, the wall, in which they occur, appears beaded in cross-section. In cells, such as the phloem elements for example, that have only a primary wall when fully differentiated, the primary pit fields alter with maturation (see Chapter 8).

A characteristic feature of the primary pit fields of living cells is the presence of concentrations of very thin protoplasmic strands, i.e. the *plasmodesmata*. The plasmodesmata connect the protoplasts of neighbouring cells (Fig. 10, no. 3). They are apparently present in all living cells of higher plants, the living protoplasts of which are, therefore, united to form a single unit. Because of their extreme fineness and their plasmic nature, plasmodesmata can be seen, in the light microscope, only when special techniques are used. Plasmodesmata are relatively easily seen in the endosperm of seeds, such as those of the *Phoenix*, *Aesculus* and *Diospyros* and in the cotyledons of some plants.

Plasmodesmata usually occur in groups, but sometimes they may be more or less evenly distributed over the entire wall. When in groups the plasmodesmata usually occur in the primary pit fields as has been demonstrated in cambial cells (Kerr and Bailey, 1934; Livingston and Bailey, 1946). In mature living cells with secondary walls large groups of plasmodesmata traverse the pit membranes.

The cytoplasmic nature of the plasmodesmata is proven by the following facts: they are present only in living cells; they stain similarly to the cytoplasm; they exhibit a positive reaction for oxidases; on plasmolysis the protoplast withdraws from the wall in all places except where plasmodesmata are present (Esau, 1953).

The following explanation of the origin and development of the plasmodesmata has been given by Frey-Wyssling (1959). The nature of the cell plate is unknown but without doubt it is partly protoplasmic. It is thought that young growing walls are penetrated by cytoplasm. With the accumulation of the cellulose microfibrils (Fig. 16, no. 2) and pectic substances in the wall, the cytoplasmic connections gradually become narrower until they constitute thin threads, i.e. the plasmodesmata. According to Buvat and Puissant (1958) plasmodesmata are already present in the cell plate at the time of cell division. Apparently, with the increase of the wall surface the number of plasmodesmata also increases; this is probably brought about by the splitting of the original threads. When new areas of

contact are made between the cells (during the expansion of tissues, during intrusive growth, in grafts, connections between tyloses, etc.), new plasmo-

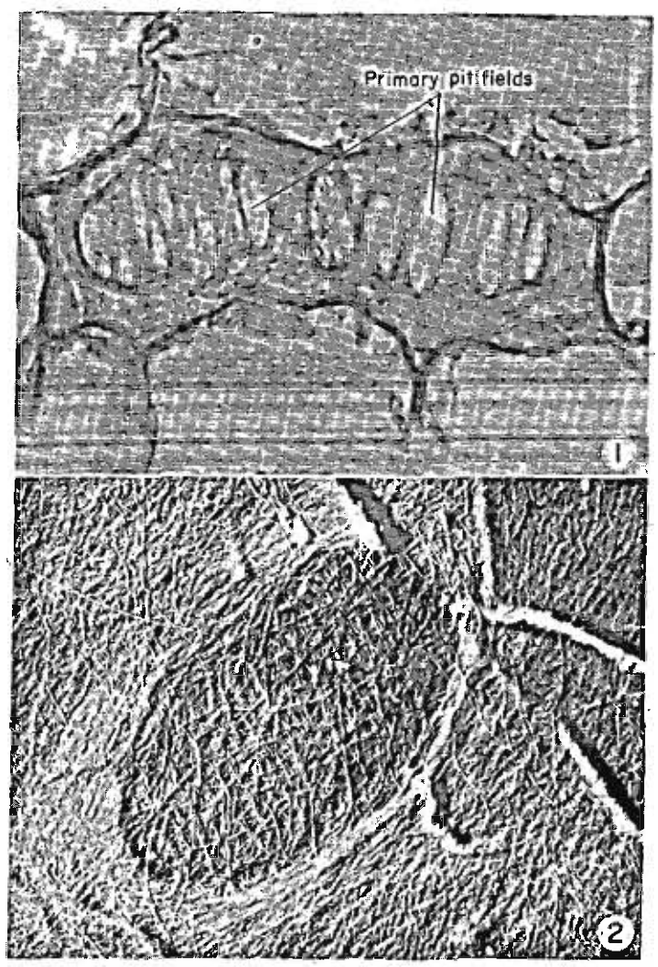

FIG. 16. 1, Micrograph of parenchyma cells from the pith of *Nicotiana tabacum* showing primary pit fields. ×750. 2, Electron micrograph of a primary pit field of *Zea mays*. ×24,000. (No. 2, after Mühlethaler, 1950.)

desmata are apparently formed in the maturing cell walls. Plasmodesmata have been seen to become branched during the expansion and thickening of the longitudinal walls of the cortical cells in [illegible]

1960). Branched plasmodesmata have also been observed by the author in the pit membranes of the wood fibres of *Tamarix* spp.

It is thought that the plasmodesmata play an active role in the transport of materials and the relay of stimuli. According to Schumacher (1942) one of the proofs that plasmodesmata relay stimuli is their presence in the outer walls of the epidermal cells. It is also thought that viruses can pass from one cell to another via the plasmodesmata (Esau, 1961).

Pits

Certain portions of the cell wall remain thin even as the secondary wall is formed and they, therefore, consist only of primary wall material. These areas, which are of variable shape, are called *pits* (Fig. 17, nos. 1–6). Some authors use the term pit to refer only to the pit cavity together with the primary wall, which closes the pit. Others use the term pit to refer to the above structures together with that part of the secondary wall that surrounds the pit cavity. Pits can develop over the primary pit fields and then one or more pits may develop in the pit field, or pits develop on those parts of the primary wall devoid of pit fields. On the other hand, the primary pit fields can become completely covered by the secondary cell wall.

The pits are apparently areas through which substances pass from cell to cell. The concentration of plasmodesmata, in living cells in the region of the pit membranes is an additional proof of the pit being a channel of exchange. Generally each pit has a complementary pit exactly opposite it in the wall of the neighbouring cell. Such pits form a morphological and functional unit called the *pit-pair* (Fig. 17, no. 2). The cavity formed by the break in the secondary wall is called the *pit cavity*. The membrane, built of the primary cell walls and middle lamella, that separates the two pit cavities of the pit-pair, is called the *pit membrane* or *closing membrane*. The opening of the pit on the inner side of the cell wall, i.e. on that side facing the lumen of the cell, is called the *pit aperture* (Fig. 17, no. 2).

Two principal types of pits are recognized—*simple pits* and *bordered pits* (Fig. 17, nos. 1–7). The main characteristic of bordered pits is that the secondary wall develops over the pit cavity to form an overarching roof with a narrow pore in its centre. In a simple pit no such development of the secondary wall is present.

If the two pits of a pair are simple, a *simple pit-pair* is formed (Fig. 17, no. 2); if the two pits are bordered, a *bordered pit-pair* (Fig. 17, no. 3); if one of the pits is simple and the other bordered, a *half-bordered pit-pair* (Fig. 17, no. 4). If the pit has no complementary pit in the adjacent cell or if it is opposite an intercellular space, it is termed a *blind pit* (Fig. 17, no. 1). Sometimes two or more pits are found opposite one large pit—such an arrangement is called *unilateral compound pitting*.

The pit cavity of a simple pit may have the same diameter over its entire depth, or it may widen or narrow toward the pit aperture. In places where the secondary wall is very thick the pit cavity has the form of a canal.

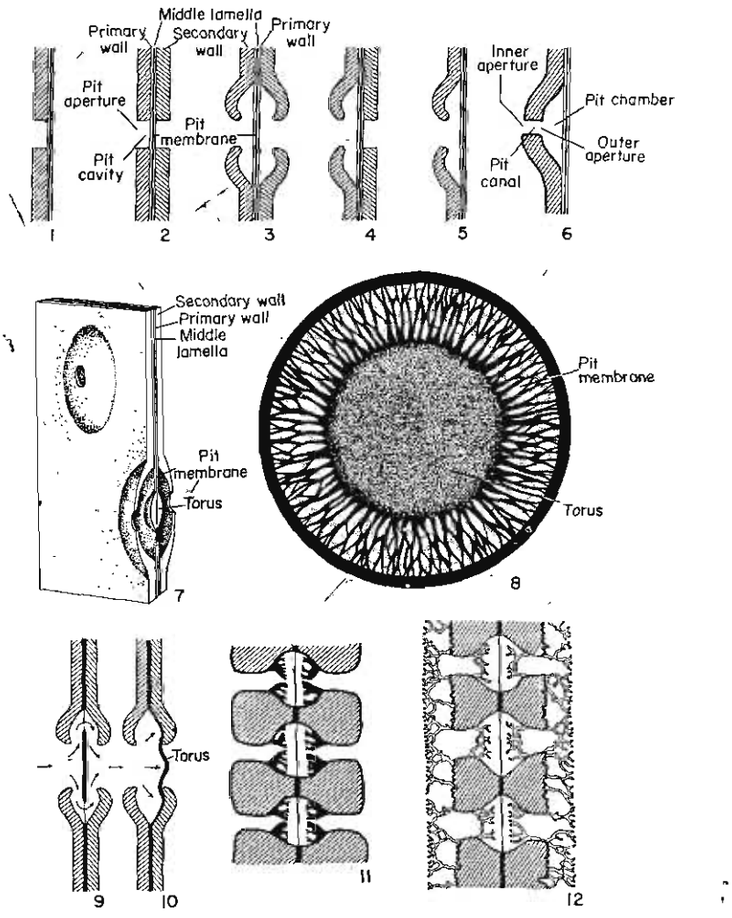

FIG. 17. Structure of pits. 1, Simple pit. 2, Simple pit-pair. 3, Bordered pit-pair. 4, Half-bordered pit-pair. 5 and 6, Bordered pits. 7, Three-dimensional diagram of a portion of the adjacent walls of two tracheids showing the structure of bordered pit-pairs. 8, Diagram of pit membrane and torus of *Pinus* showing the perforations in the membrane. 9 and 10, Longitudinal sections of bordered pit-pairs of a tracheid. Arrows indicate direction of water flow. 9, Torus and membrane in median position. 10, Torus closing one of the pit apertures. 11 and 12, Longitudinal section of the wall of adjacent vessels with vestured pits. (Nos. 8–12 after I.W. Bailey.)

Sometimes this canal is branched towards the outer layers of the cell wall and then the pit is called a *branched simple pit*. Such pits arise from the fusion of several pits during the centripetal addition of layers to the secondary wall (Fig. 38, no. 4).

Simple pits are usually found in parenchyma cells with thickened walls, in libriform fibres and sclereids. Bordered pits are found in the tracheary elements and in fibre-tracheids.

The bordered pit is more complicated than the simple in its structure and is variously shaped. In the bordered pit that part of the pit cavity that is formed by overarching of the secondary wall is called the *pit chamber* and the opening in the secondary wall that faces the cell lumen is called the *pit aperture*. If the secondary wall is very thick a canal—the *pit canal*—is formed between the cell lumen and the pit chamber. In the pit canal two openings are distinguished—that facing the cell lumen is termed the *inner aperture* and that nearest the pit chamber, the *outer aperture* (Fig. 17, no. 6).

In some plants there are bordered pit-pairs in which the pit membrane is thickened in its central portion; this thickening, which is of a primary nature, is disc-shaped and is termed the *torus* (Fig. 17, nos. 7–10). The diameter of the torus is wider than that of the pit aperture.

Bannan (1941) describes the occurrence of thickenings, other than the torus, on the pit membrane. These thickenings may be radial or tangential in relation to the torus. The torus found in the bordered pits of *Cedrus* is fringed on its circumference (Fig. 10, no. 2). This feature is a characteristic of *Cedrus*, and as such it aids in the identification of the wood of this genus.

In tracheids of many conifers the pit membrane around the torus is porous. The presence of these pores was discovered in 1913 by Bailey in experiments that demonstrated the passage of a suspension of finely divided particles of carbon from one tracheid to another. This has been confirmed by electron micrographs (Liese and Fahnenbrock, 1952). The pit membrane is usually flexible and, under certain conditions, the torus can be pushed against one of the pit apertures (Fig. 17, nos. 9, 10). When the torus is in the median position, i.e. in the middle of a pit-pair, water can easily pass from one tracheid to another. In a pit-pair where the torus is in a lateral position, i.e. pressed against one of the pit apertures, the passage of water is very limited. Most of the tori in late wood and all of them in the heartwood are always in a lateral position and the flexibility of the pit membrane is lost.

The presence of a torus is especially characteristic of the bordered pits of the Gnetales, of *Ginkgo*, and most of the Coniferales. Tori occur only rarely in the Ophioglossales (Bierhorst, 1960) and in the angiosperms.

In some dicotyledons thin, simple or branched sculpturings are present on the secondary wall that forms the pit chamber, or around the pit aperture. Such pits are called *vestured pits* (Fig. 17, nos. 11, 12) and the sculp-

turings may have various shapes. Because of the special properties of light refraction and of staining these pits appear as if porous or net-like in surface view and, thus, were once termed sieve-pits. Vestured pits are found in the tracheary elements of the secondary wood of certain dicotyledonous genera and species, such as sōme of the Leguminosae, Cruciferae, Myrta-

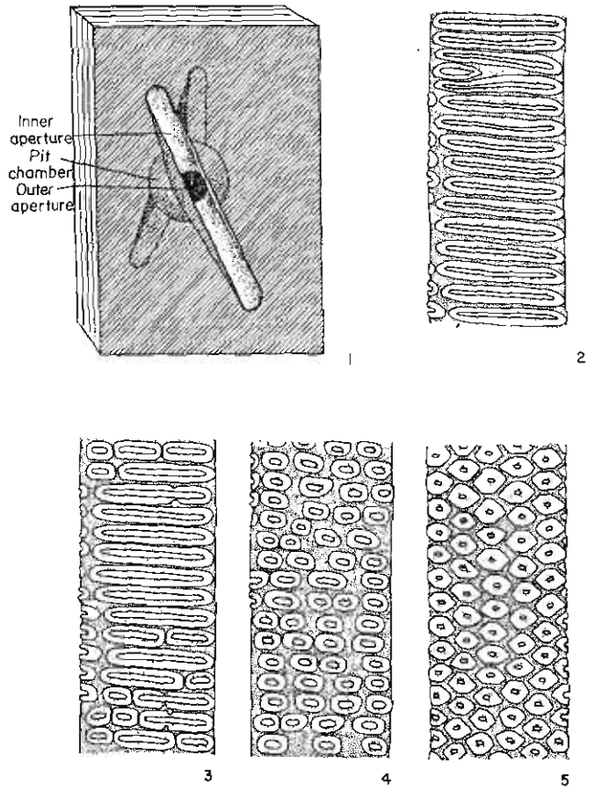

FIG. 18. 1, Portion of the common wall between two fibre-tracheids showing the type of bordered pit characteristic of these elements. 2–5, Types of pitting. 2, Scalariform pitting. 3, Transition from elongated pits in scalariform arrangement to shorter circular pits in opposite arrangement. 4, Opposite pitting. 5, Alternate pitting.

ceae and Caprifoliaceae. Vestured pits are found in phylogenetically more developed xylem and therefore they are considered to be an advanced form of pit.

The shape of the pit aperture can be the same as that of the pit chamber or different from it. The pit aperture may be round, elliptic or linear. As

the walls continue to thicken the pit chamber becomes smaller and the pit canal between the inner and outer apertures becomes longer. In such pits the inner aperture often becomes long and narrow, as seen in surface view, and, in very thick walls, its longitudinal axis may be longer than the diameter of the pit chamber. When the inner aperture is large and linear, narrow or elliptic, and when the outer aperture is small and circular, the pit canal has the shape of a flattened funnel. The elongated inner apertures of such a bordered pit-pair may be parallel or crossed. This type of pit occurs mainly in fibre-tracheids (Fig. 18, no. 1).

Bordered pits found in tracheary elements vary in shape and arrangement. When the pits are distinctly elongated or linear and arranged in ladder-like tiers the arrangement is termed *scalariform pitting*. When the pits are circular or only slightly elongated and the outlines are elliptic there are two possible ways in which they may be arranged on the wall: in horizontal lines, i.e. *opposite pitting*, or in diagonal lines, i.e. *alternate pitting*. When the pits are crowded the outline of the opposite pits becomes rectangular or square, and that of the alternate pits hexagonal (Fig. 18, nos. 2–5).

Tracheary elements have especially well developed bordered pits in those regions where they are adjacent to other tracheary elements. In the regions of contact with parenchymatous cells reduced bordered pits are sometimes found. Usually those parts of the wall adjacent to fibres are devoid of pits.

Other sculpturings on the cell wall

In addition to the pits many other sculpturings exist on the cell walls. These include, for example, the perforations in the end walls of the vessel members, various thickenings on the inner surface of cell walls, such as wall thickenings in the protoxylem elements, spiral thickenings on the inner surfaces of pitted secondary walls, casparian strips of endodermal cells, thickenings in the walls of the endothecial cells of pollen sacs, and external projections formed partly by the wall itself and partly by deposits, e.g. of cuticle on epidermal cells and of external layers on spores and pollen grains. The above features are discussed in later chapters. Here only three structures will be discussed—*crassulae*, *trabeculae* and *wart structures*.

Crassulae are linear or crescent-shaped thickenings of the primary wall and middle lamella which occur between bordered pits or small groups of these pits. The crassulae may sometimes surround the pits. They represent the borders of the primary pit fields of the young cell from which the element developed. Crassulae are well developed in the tracheids of certain gymnosperms (Fig. 133, no. 4).

Trabeculae are rod-shaped thickenings of the wall which traverse the cell lumen radially. They usually appear in radial rows in the wood ele-

ments, and sometimes continuous rows of cells traversed by trabeculae extend through the cambium into the phloem. Trabeculae are common in the tracheids of the secondary wood of conifers.

Wart structures are structures that have been observed on the inner surface of the secondary wall of conifer tracheids and of fibres and vessels of many dicotyledons (Wardrop *et al.*, 1959; Liese and Ledbetter, 1963). The diameter of these structures varies between 0·1 μ and 0·5 μ. They develop after, or towards the completion of, differentiation and lignification of the secondary wall, and according to Liese and Ledbetter they consist of remnants of the protoplast. These structures are probably identical with the tertiary layer as described by Frey-Wyssling (see p. 24).

Cystoliths

In some dicotyledonous families, such as the Moraceae and Urticaceae, stalked outgrowths of the wall that project into the cell lumen are present. These outgrowths are called *cystoliths*. They consist of cellulose and are impregnated with calcium carbonate. Cystoliths are irregular in shape and sometimes they almost completely fill the cell. Cystoliths may appear in parenchymatous cells in various parts of the plant including even the xylem and phloem rays, but they are usually found in the epidermis in hairs or special large cells which are termed *lithocysts* (Fig. 55, no. 1).

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CHAPTER 3

MERISTEMS

IN THE early stages of the development of the embryo, all the cells undergo division, but with further growth and development cell division and multiplication become restricted to special parts of the plant in which the tissues remain embryonic in character and the cells retain the ability to divide. These embryonic tissues in the mature plant body, are called *meristems*. Cell division can also occur in tissues other than meristems, for instance, in the cortex of the stem and in young, developing vascular tissues. However, in these tissues the number of divisions is limited. On the other hand, the cells of the meristems continue to divide indefinitely and as a result new cells are continually added to the plant body. Meristems may also be found in a temporary resting phase, for instance, in perennial plants that are dormant in certain seasons and in axillary buds that may be dormant even during the active phase of the plant.

The process of the growth and morpho-physiological specialization of the cells produced by the meristems is called *differentiation*. Theoretically, it was believed that the tissues that undergo differentiation gradually lose the embryonic characteristics of the meristem and acquire the mature state. Such tissues are called *mature* or *permanent*. Recently it has been shown that the term permanent tissues can only be used in relation to certain cells which have undergone irreversible differentiation, as, for instance, sieve elements which have no nucleus and dead cells, such as tracheids, vessel elements and cork cells. All cells which contain nuclei possess, to a certain degree, the ability to grow and divide and redifferentiate if the appropriate stimulus is present (Bloch, 1941; Buvat, 1944, 1945; Gautheret, 1945, 1957; White, 1946; Wetmore, 1954, 1956).

Classification of meristems

The classification of meristems is made on the basis of various criteria —their position in the plant body, their origin and the tissues which they produce, their structure, their stage of development and their function.

According to the position of the meristems in the plant body they are divided into the following types: (a) *apical meristems*, which are found in

the apices of the main and secondary shoots and roots; (b) *intercalary meristems*, which are found between mature tissues, as, for example, in the bases of the internodes of grasses; (c) *lateral meristems*, which are situated parallel to the circumference of the organ in which they are found, as, for instance, the vascular cambium and the phellogen.

It is customary to distinguish between *primary* and *secondary meristems* —a classification based on the origin of the meristems. Accordingly, primary meristems are those whose cells develop directly from the embryonic cells and so constitute a direct continuation of the embryo, while secondary meristems are those that develop from mature tissues which have already undergone differentiation.

The above definitions of primary and secondary meristems, however, are not always accurate. For example, the apical meristems of truly adventitious organs develop secondarily within relatively mature tissues as well as within secondary meristematic tissues, although according to their structure and function they are primary meristems. On the other hand, a large part of, or sometimes even the entire, vascular cambium, which is generally accepted to be a secondary meristem, develops, at a late stage, from the apical meristem, i.e. from a part of the procambium.

Examples of secondary meristems, which can be determined as such without doubt, according to origin, are the phellogen which develops from parenchyma or collenchyma cells which have already undergone differentiation and callous tissue which develops in tissue cultures made from mature tissues.

From the above it can be seen that it is more correct to use the terms primary and secondary meristems to refer to the stage of development at which the meristems appear and to the types of tissue that develop from them and not to their origin. From the primary meristems the fundamental parts of the plant, such as the epidermis, the cortical tissues of the stem and root, the mesophyll of the leaf and the primary vascular tissues develop, and from the secondary meristems the secondary vascular and protective tissues.

In certain monocotyledons, such as some palms, banana, *Veratrum* and others, the thickening of the stem takes place near the apices and therefore is regarded as being of primary nature. The meristem responsible for this type of increase in thickness is termed *primary thickening meristem.*

Stages of development of primary meristems

Secondary meristems, e.g. the cambium and the phellogen, are homogeneous tissues in which different stages cannot be distinguished. In the primary meristems, however, different regions in various stages of differentiation can be distinguished. [illegible]

a *promeristem* and a meristematic zone below it in which groups of cells have undergone a certain degree of differentiation. The promeristem consists of the *apical initials* together with the cells derived from them and which are still close to the initials. The partly differentiated meristematic zone consists of the following three meristems: the *protoderm* from which the epidermal system of the plant develops, the *procambium* from which the primary vascular tissues develop, and the *ground meristem* from which the ground tissues of the plant, as, for instance, the parenchyma and sclerenchyma of the cortex and pith and the collenchyma of the cortex, develop.

The term initials in meristems refers to cells which remain within the meristem and which add cells to the plant body by means of division.

Cytological characteristics of meristems

Meristematic cells are usually thin-walled, more isodiametric in shape than the cells of mature tissues and relatively richer in protoplasm. However, it is not possible to find a general morphological criterion by which meristematic cells can be distinguished from unspecialized mature cells. Usually the protoplasts of meristematic cells are devoid of reserve materials and crystals and the plastids are in the proplastid stage. However, the protoplasts of the phellogen, a secondary meristem, may contain these bodies. In most cells of apical meristems of a large number of plants, and especially among the angiosperms, the vacuoles are very small, not obvious, and are scattered throughout the protoplast. However, in pteridophytes and many spermatophytes at least some of the cells of the apical meristem contain conspicuous vacuoles. Also the cells of the vascular cambium are highly vacuolated (Bailey, 1930). In general, it is possible to state that the larger the meristematic cell, even if it is an initial cell or one close to the initials, the greater is the degree of vacuolization. The size of the meristematic cells varies. Also the ratio between the size of the cell and that of the nucleus varies very greatly in different meristematic cells. The wall of meristematic cells is usually thin, but certain cells in the apical meristems have thick walls and cells of the vascular cambium have very thick radial walls at certain periods.

From the above it can be seen that morphological analysis alone is not sufficient to determine the meristematic nature of cells and the use of experimental methods is often necessary.

Apical meristems

In the nineteenth century research workers mainly dealt with the problem of the number of the initials in the apices and the determination of the tissues that were derived from them. Thus the *histogen theory* of Hanstein

(1868) and the *apical cell theory* of Nägeli (1878) were developed. Modern research on spermatophytes deals with histo-cytological arrangement of the zones of cells and their activity in the apices. Recently experimental research on apices attached to entire plants or grown as tissue cultures has contributed to the clarification of these problems (Ball, 1946, 1947, 1960; Clowes, 1953, 1954; Wetmore, 1954, 1956; Wardlaw, 1957; Gifford and Tepper, 1962a, b). Initials can be recognized by microscopical investigations and by the use of assumptions based on the orientation of cell divisions. Experiments have been made to determine the location and number of the initials by the application of colchicine. Using this substance it has been possible to increase the number of chromosomes in a few cells, and as the derivatives of such cells possess the increased number of chromosomes it is possible to identify all the cells that are derived from the colchicine-affected cells. If the affected cell is an initial, entire regions of tissues, the cells of which have the increased chromosome number, result; thus polyploid chimeras are artificially formed. This phenomenon makes it possible to identify the initials (Dermen, 1945, 1947, 1948, 1951). Although the initials are usually permanent, opinions exist that they may sometimes be replaced by new initials. In addition to the above-mentioned studies of Dermen, the observations of other workers on polyploid chimeras (Satina et al., 1940; Satina and Blakeslee, 1941, 1943; Satina, 1959) and on variegated chimeras (Thielke, 1948, 1954, 1955, 1957; Bartels, 1960; Moh, 1961) are of great importance in the study of apical meristems.

In this book the apical meristem will be divided, as already mentioned, into two main regions—the promeristem which comprises the apical initials and neighbouring cells, and the meristematic zone below it in which the three basic meristems (the protoderm, procambium and ground meristem) of the tissue systems can be distinguished.

The following discussion deals mainly with the arrangement and function of the cells in the promeristem.

VEGETATIVE SHOOT APEX

Wolff, in 1759, discovered that the new leaves and tissues of the stem arise in the very apex of the stem. He termed this region the "punctum vegetationis". Today the term *shoot apex* is generally used (Fig. 19, no. 1) as it is the region of initiation of the primary organization of the shoot in which the processes of growth take place and which cannot be limited to a point. The shoot apex proper is considered as that terminal part of the shoot immediately above the uppermost leaf primordium. There are great differences in the shape and size of the shoot apices among the spermatophytes. In a median longitudinal section the apex generally appears more or less convex. In *Anacharis* and *Myriophyllum* and some grasses the shape

of the apex is a narrow cone with a rounded tip (Fig. 20, nos. 1, 3; Fig. 21, nos. 1, 2), while in a few plants, e.g. *Drimys* and *Hibiscus syriacus*, it is slightly concave (Gifford, 1950; Tolbert, 1961).

Before the initiation of each leaf the apical meristem widens considerably and after the appearance of the leaf primordium it again becomes narrow.

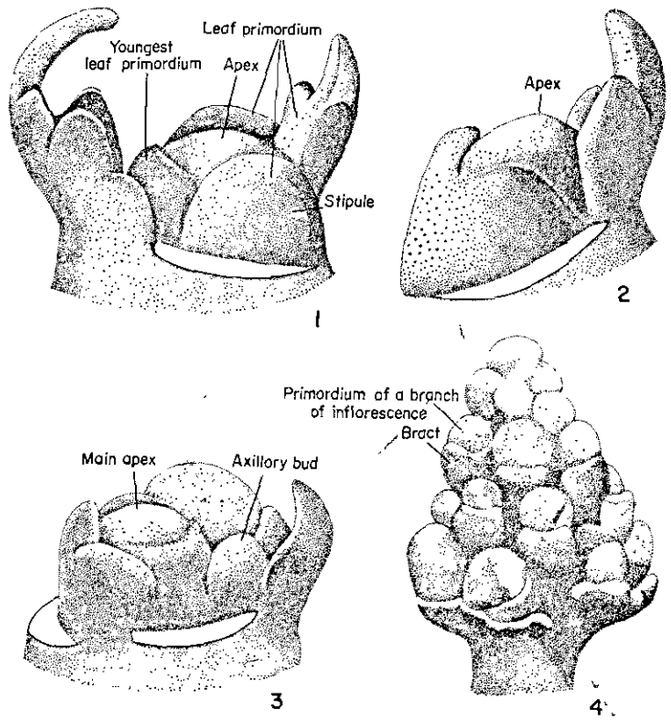

FIG. 19. Shoot apex of *Vitis vinifera*. 1, Vegetative shoot apex. 2, Vegetative shoot apex in which the tip of the apex is seen to be asymmetrical; this is apparently connected with the initiation of an axillary bud. 3, Apex in which the main apex and an axillary bud can be distinguished; the axillary bud is apparently reproductive. 4, Primordial inflorescence (Drawings adapted from Z. Bernstein.)

This phenomenon is rhythmic, i.e. it recurs with the initiation of each leaf or pair of leaves. Schmidt (1924) introduced the terms minimal- and maximal-areas of the apex. For the period between the successive initiations of two leaves or two pairs of leaves he suggested the use of the term *plastochron* (Fig. 27, nos. 1–6) which had been used previously but with a much wider meaning. The shoot apices of dicotyledons with opposite leaves (such as *Lonicera, Coleus, Vinca, Ligustrum, Syringa* and others) are particularly suitable for the study of plastochronic changes.

In the Angiospermae the shoot apices are usually small. The measurement of the diameter is taken as the width of the apex immediately above

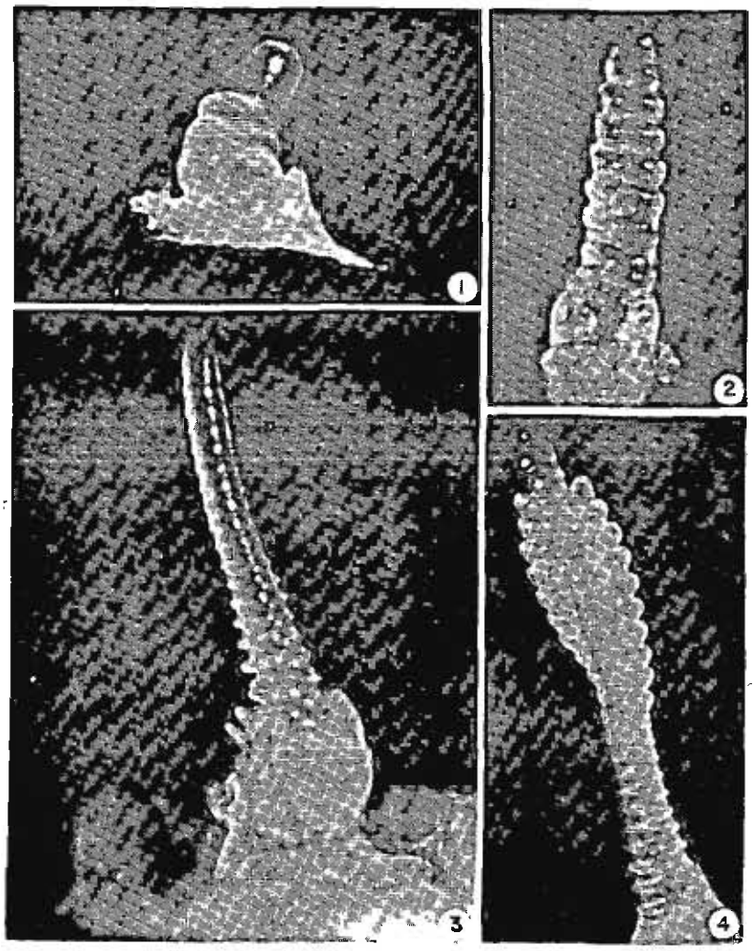

FIG. 20. Photographs of shoot apices. 1, Vegetative shoot apex of *Hordeum bulbosum*. 2, Early stage in development of inflorescence of *Hordeum bulbosum*. 3, Shoot apex of *Secale* at the time of floral induction. 4, Early stage of floral development in *Secale*. (Photographs courtesy of D. Koller.)

the youngest primordium. The diameter usually varies between 90 μ (in certain grasses) and 130–200 μ (in many dicotyledons). In the banana plant, however, width of the apex reaches 280 μ, in certain Palmae and in *Nym-*

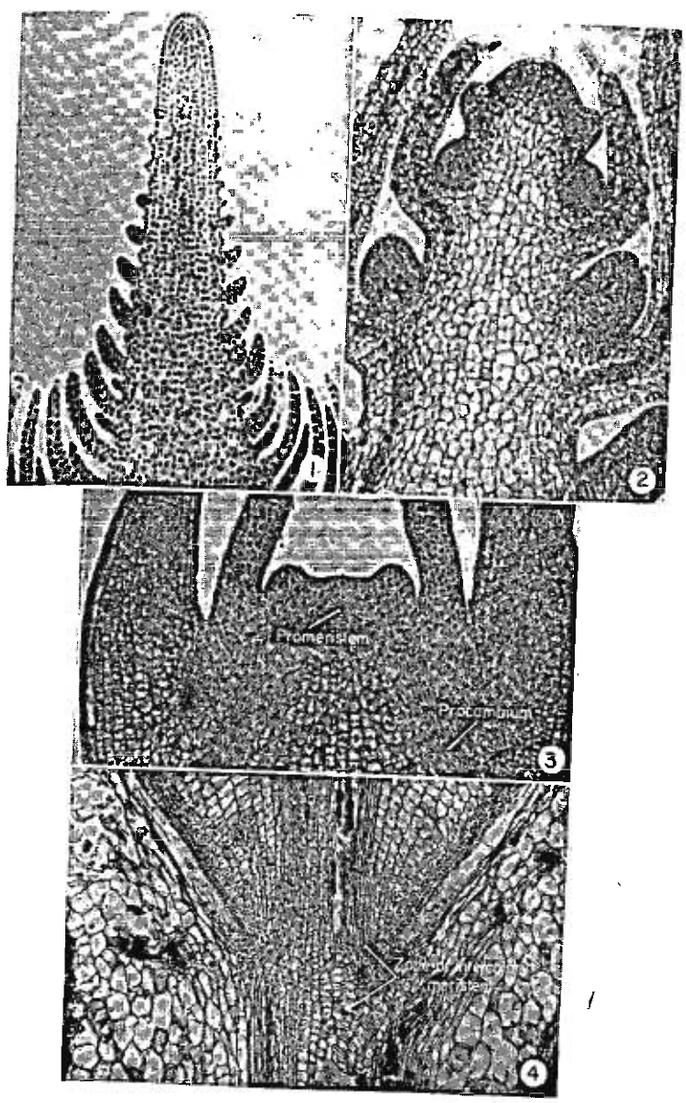

FIG. 21. 1–3, Micrographs of longitudinal sections of vegetative shoot apices. 1, *Anacharis canadensis*. ×30. 2, *Coleus blumei*. ×135. 3, *Vinca major*. ×80. 4, Portion of a median longitudinal section of the shoot of *Anabasis articulata* showing the intercalary meristem at the base of the internode. ×45.

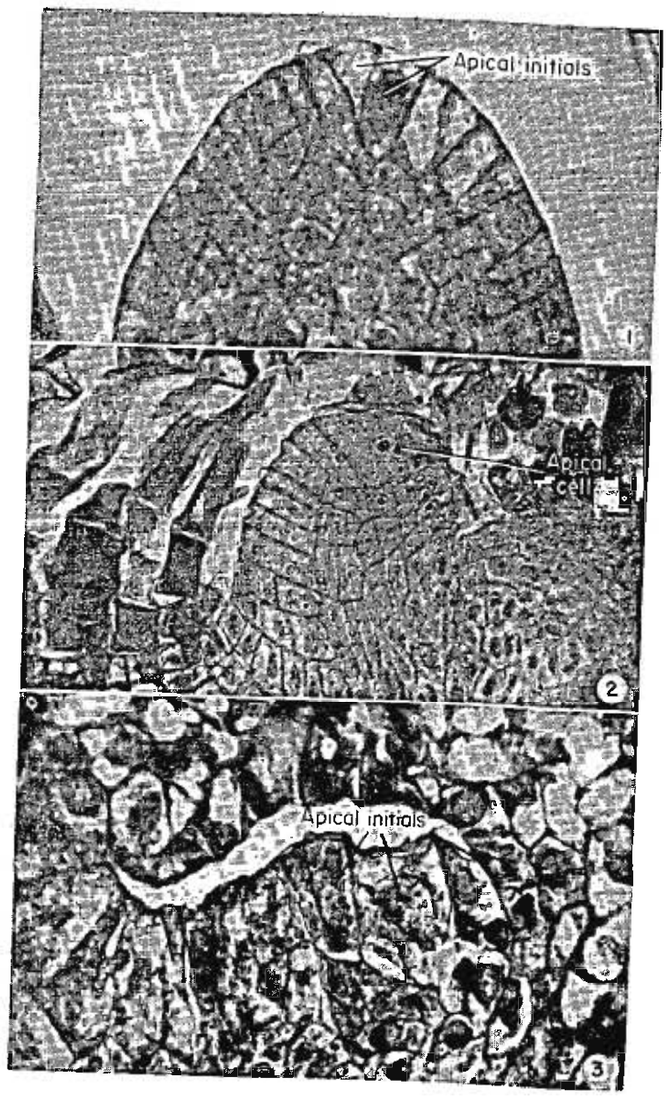

FIG. 22. Micrographs of longitudinal sections of shoot apices of pteridophytes. 1, *Selaginella*, in which two apical initials can be distinguished. ×1150. 2, *Marsilea* with a single apical initial. ×430. 3, *Ophioglossum lusitanicum* with several apical initials. ×380.

phaea, 500 μ, and in *Trichocereus* it is between 700–800 μ (Ball, 1941; Boke, 1941; Cutter, 1957; Fahn *et al.*, 1963). The differences in the diameter of the apices of gymnosperms are much greater (Kemp, 1943). The apices of the conifers are cone-shaped and fairly narrow and the dimensions of their diameter are similar to those typical for angiosperms. On the other hand, the apices in *Ginkgo* and *Cycas* are three to eight times as wide as they are high (Johnson, 1944). In *Cycas revoluta* the diameter of the maximal-area of the apex is 3·5 mm (Foster, 1940).

SHOOT APEX OF PTERIDOPHYTES

In the Pteridophyta there are one or more initials which can usually be easily distinguished from the neighbouring cells. These initials give rise to all the cells of the apex. If only one initial is present it is termed the *apical cell* (Fig. 22, no. 2) and if more than one cell are present they are termed *apical initials* (Fig. 22, no. 3). The single apical cell usually is tetrahedral in shape and its base is directed toward the surface of the apex. A single apical cell is found in the Psilotales, in *Equisetum* and in some ferns. The single apical cell divides in such a manner that the new cells are

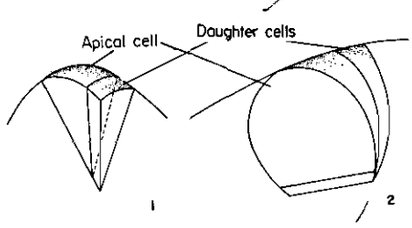

FIG. 23. *Diagrams of apical cells to show the manner of division and addition of* cells to the plant body. 1, Tetrahedral apical cell with base directed towards the surface of the apex and in which the planes of division are parallel to the other three faces. 2, Apical cell in which the planes of division are parallel to two faces only. (Adapted from Schüepp, 1926.)

formed on all its sides with the exception of that on the surface of the apex. The apical cells of pteridophytes are usually four-sided, but in some water ferns, e.g. *Salvinia* and *Azolla*, and sometimes in *Selaginella*, they are only three-sided. In the former, new cells are produced on three sides while in the latter only on two sides (Fig. 23, nos. 1, 2).

It is thought that the ferns (*Filicinae*) with a single apical cell are evolutionarily more advanced than those with several apical initials.

SHOOT APEX OF GYMNOSPERMS

It was believed that the tissue of the shoot apex of spermatophytes was a primordial meristem (promeristem) consisting of undifferentiated cells which are morphologically equal. Recent cyto-histological research on the shoot apices of spermatophytes has disproved this theory and has shown that it is possible to distinguish, in these meristems, a complicated arrangement of groups of cells which are characterized by the following features—the size of the cell and the nucleus, differential staining, the relative thickness of the cell walls and the frequency and orientation of cell division. The plane of these divisions may be anticlinal, i.e. at right-angles to the surface of the apex, or periclinal, i.e. parallel to the surface of the apex, or diagonal.

Since 1937 much research has been made on the structure of the shoot apex of gymnosperms (Korody, 1937; Foster, 1938, 1939b, 1940, 1943; Cross, 1939, 1942, 1943; Johnson, 1939, 1944; Gifford, 1943; Kemp, 1943; Majumdar, 1945; Sterling, 1945, 1946; Allen, 1947; Gifford and Wetmore, 1957; Guttenberg, 1961).

It is characteristic of all the gymnosperms that the direction of the cell divisions in the surface of the apex is both anticlinal and periclinal and so this layer represents the initiation zone of the entire apex and has been termed the *surface meristem*. The striking feature in the structure of most gymnosperm apices is the occurrence of a distinct zone of *central mother cells*. The cells of this zone are characterized by their size, the numerous large vacuoles and the presence, in many of them, of relatively thick walls. Along the sides and the base of the central mother cell zone the other apical regions develop as a result of the diagonal and horizontal divisions of the central mother cells. In this way the *peripheral zone* or *flank meristem* is developed laterally and the *rib meristem* zone (also known as *central meristem*) from the base. The term rib meristem was introduced by Schüepp (1926) to describe that type of meristematic tissue that consists of vertical series of transversely dividing cells. According to Popham (1952), three principal types of gymnosperms can be distinguished on the basis of the structure of the shoot apex (Fig. 24, nos. 4–6; Fig. 25, nos. 1, 2).

1. The *Cycas* type (Fig. 24, no. 4) in which three meristematic zones can be distinguished. (a) The *surface meristem* in which the cells divide anticlinally, periclinally and diagonally. The cells of this zone are not uniform in appearance and apical initials have been distinguished in the centre of this zone in the seedlings of *Cycas revoluta*, but not in mature plants. The cells of this zone give rise to the epidermis and the other apical meristematic zones. (b) The *rib meristem* which is situated in the central region of the apex below the surface layer. In the upper region of this zone vertical rows of cells are obvious. The cells at the base of these rows divide periclinally, anticlinally and diagonally, and they are usually large and contain large

vacuoles. In *C. revoluta* the pith develops from this tissue. (c) The *flank meristem* which enlarges by cell division within the zone itself and by the addition of cells from the surface layer and from the periphery of the rib meristem. The cells of this zone are smaller than those of the rib meristem and they are generally elongated. In *C. revoluta* the cortex, the procambium and the leaf primordia develop from this zone.

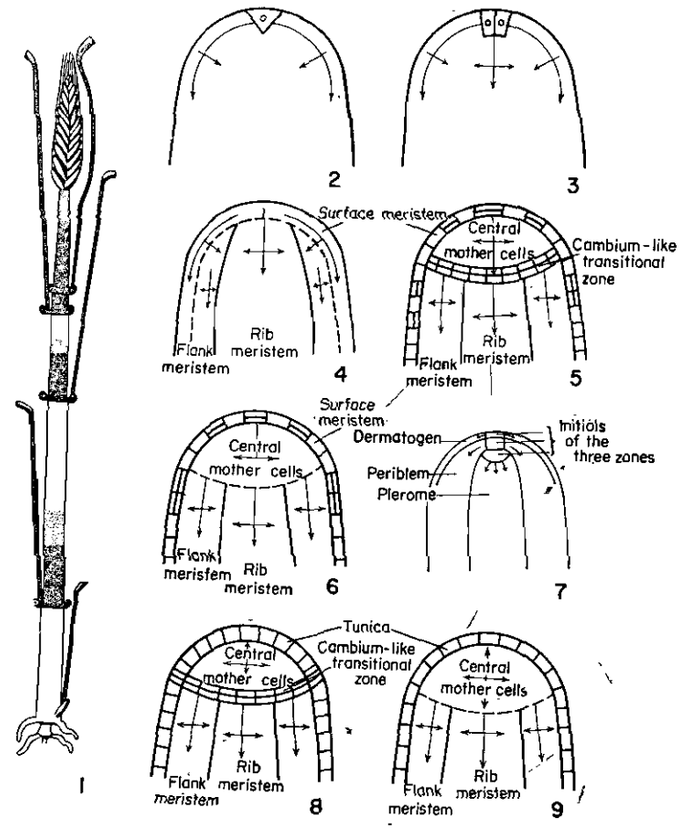

FIG. 24. 1, Schematic drawing of a grass plant to show the regions of growth. Intercalary meristematic regions, heavily shaded; regions that are still growing but whose tissues have undergone a certain degree of differentiation, lightly shaded; mature regions, unshaded. 2–9, Diagrams of cyto-histological zonation in vegetative shoot apices. 2, Pteridophyte type with single apical cell. 3, *Selaginella* type with 2–5 apical initials. 4, *Cycas* type. 5, *Ginkgo* type. 6, *Cryptomeria-Abies* type. 7, Schematic representation of the histogen theory of angiosperms. 8, *Opuntia* type. 9, Usual angiosperm type. (No. 1, adapted from Esau, 1953; nos. 2–6, 8 and 9, adapted from Popham, 1952.)

2. The *Ginkgo* type (Fig. 25, no. 1) in which five meristematic zones can be distinguished in the apex. (a) The *surface meristem*, the cells of which mostly divide anticlinally, but among which periclinal divisions also occur. The periclinal divisions are more frequent in the cells of the summit.

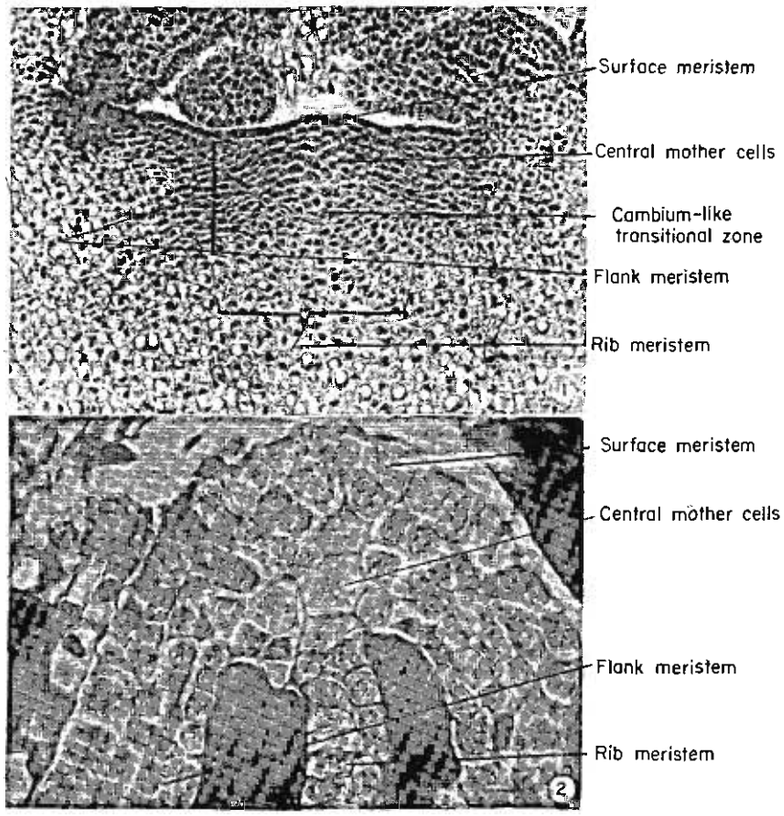

FIG. 25. Micrographs of longitudinal sections of gymnosperm shoot apices. 1, Shoot apex of *Ginkgo* in which five zones can be distinguished. × 80. 2, Shoot apex of *Pinus halepensis* in which four zones can be distinguished. ×400. (Dark-staining areas are resin-filled cells.)

These cells are the *apical initials*. (b) The zone of *central mother cells* which occurs in a median position below the surface layer. These cells are large, polyhedral and they are irregularly arranged. They contain numerous vacuoles and the nuclei of many of them are large and the cell walls are thick, particularly in the angles of the cells. The division of these cells

is in various planes. (c) The *cambium-like transitional zone* which is cup-shaped. This zone, which forms a transitional zone between the central mother cells and the zones below them, is relatively narrow and is characterized by frequent cell divisions. Most of the divisions are periclinal in relation to the central mother cells, and so cells are added to the zones below the transitional zone. (d) The *rib meristem* which is found under the central portion of the cambium-like transitional zone. The cells in this zone are generally arranged in rows and the pith of the stem develops from this zone. (e) The *flank meristem* which forms a cylinder surrounding the rib meristem, and which is a continuation of the cambium-like transitional zone. The number of cells in this zone increases by division in the meristem itself as well as by the addition of cells from the surface meristem and the cambium-like transitional zone. The cortex, leaf primordia, procambium and, in certain plants *(Microcycas* and *Zamia)*, the outer region of the pith develop from this zone. The following are some examples of plants with the *Ginkgo* type of apex: *Ginkgo biloba*, *Zamia* spp., *Sequoia sempervirens*, *Microcycas calocoma* (side branches) and *Pseudotsuga taxifolia*.

3. The *Cryptomeria-Abies* type (Fig. 25, no. 2). In this type four meristematic zones can be distinguished. The cambium-like transitional zone is absent and the remaining zones are as in the *Ginkgo* type. Of the plants with this type of apical meristem the following species should be mentioned: *Pinus montana*, *Sequoia gigantea*, *Metasequoia glyptostroboides*, *Abies concolor*, *Taxus baccata*, *Ephedra altissima* and *Cryptomeria japonica*.

SHOOT APEX OF ANGIOSPERMS

At the beginning of the cyto-histological research on the apices of plants the *histogen theory* of Hanstein (1868) was put forward. According to Hanstein the following three zones (Fig. 24, no. 7) can be distinguished in the shoot apex of angiosperms: an outermost zone, the *dermatogen;* a central zone, *plerome*, which consists of irregularly arranged cells; and a hollow cylindrical zone of several layers of cells between the dermatogen and the plerome, the *periblem*. Hanstein stated that the dermatogen, periblem and plerome develop from independent groups of initials, which act as direct histogens. According to this theory, therefore, the meristems are destined from the beginning to produce certain tissues, i.e. the epidermis develops from the dermatogen, the cortex and internal tissues of the leaf from the periblem, and the central cylinder from the plerome. The histogen theory of Hanstein was accepted for a long time, but later research, which brought to light the following facts, disproved it. (1) In most spermatophytes it is not possible to distinguish clearly between the periblem and plerome. (2) No predetermination of the mature tissues can be traced in the various initials. In 1924, the theory of Schmidt which divides the

apex into two regions, the *tunica* and the *corpus*, was postulated. According to this theory no constant relationship can be traced between the particular initials of the promeristem and the inner tissues of the shoot. The two regions recognized by this theory are usually distinguished by the planes of cell divisions in them. The tunica consists of the outermost layer or layers of cells which surround the inner cell mass – the corpus. The plane of cell division in the tunica is principally anticlinal. In the corpus the planes of cell division are in all directions. The tunica enlarges in surface area and the corpus in volume. The *tunica–corpus theory* is a very adaptable one and today it is generally accepted in literature.

As already mentioned, the tunica consists of a single or a few layers of cells which surround the inner meristem. The number of layers is not always constant in a given genus or family, and not even in a species, and cases are known where the number of layers varies in a single plant during different stages of the development of the vegetative apex. The number of layers can be from one to nine. In monocotyledons, no more than six have been recorded. Sometimes, especially among the monocotyledons, a few periclinal divisions occur in the tunica, which is a contradiction of the original definition of the tunica and therefore Popham and Chan (1950) introduced the term *mantle* for all the outer layers of the apex which can be distinguished histologically from the inner cell mass without taking into account the planes of division in these layers. They retained the term tunica for those layers in which only anticlinal cell divisions take place. In this book the term tunica is used in the broad sense, and is equivalent to the mantle of Popham and Chan.

Although the plane of cell division is generally the same throughout the entire tunica, cytologically two zones can be distinguished in it. One zone is the central apical zone consisting of one or few *initials* which are larger and have larger nuclei and vacuoles than the other tunica cells and which, therefore, are also more lightly staining. The second zone is that region on the sides of the apex between the initials and the leaf primordia. It consists of smaller, more darkly staining cells which divide more frequently and among which periclinal division may occur close to the primordia.

The corpus is far less homogeneous than the tunica. Among the angiosperms two main types of corpus are recognized on the basis of internal arrangement (Popham, 1952).

1. The *usual angiosperm type* (Fig. 24, no. 9) in which three main zones can be distinguished in the corpus: (a) the zone of *central mother cells* which probably represent the corpus initials and which is located below the apical portion of the tunica, i.e. below the tunica initials; (b) the *rib meristem;* and (c) the *flank meristem*. The latter two zones appear as continuations of the central mother cells (Fig. 21, nos. 1, 3).

2. The *Opuntia type* (Fig. 24, no. 8) in which, in addition to the above zones, a *cambium-like transitional zone* can be distinguished. This zone,

which is cup-shaped, is found between the central mother cells and the rib and flank meristems (Fig. 26, nos. 1, 2). The cambium-like transitional zone differs from the other zones of the apical meristem in that its height and diameter vary considerably during the plastochron, reaching a maximum development close to a developing primordium (Fahn *et al.*, 1963).

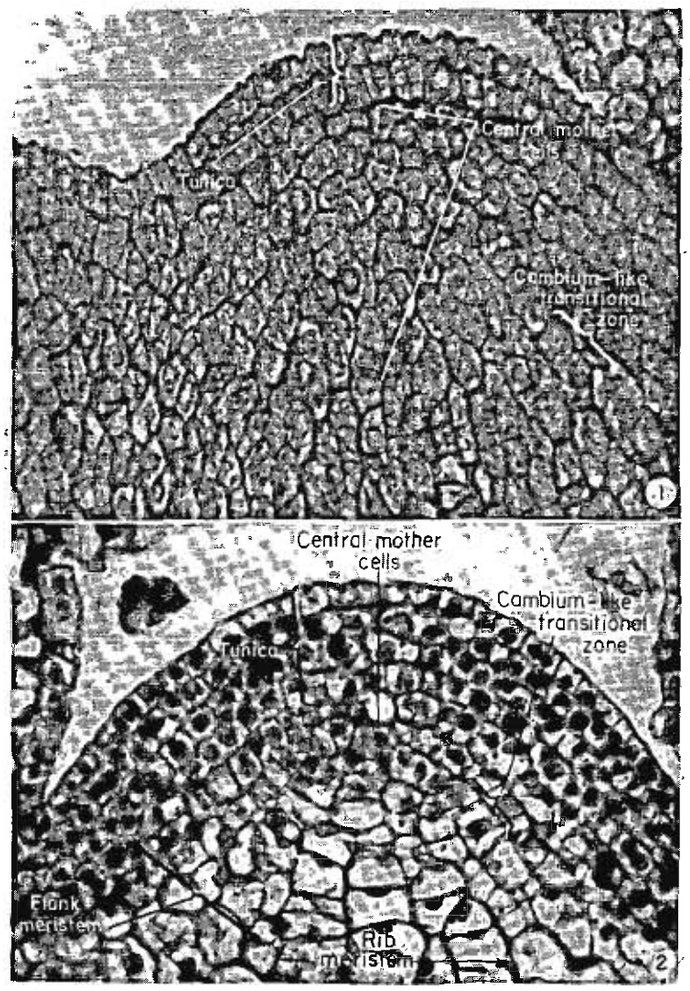

FIG. 26. 1, Micrograph of a longitudinal section of the upper portion of the vegetative shoot apex of the Dwarf Cavendish banana showing a two-layered tunica. ×460. 2, Micrograph of a longitudinal section of the shoot apex of *Coleus blumei* showing a four-layered tunica. ×450.

According to Philipson (1954) this zone is only a temporary feature in many of the plants in which it occurs, as it disappears towards the end of the plastochron.

The following are some examples of plants with an *Opuntia* type apex: *Phoenix dactylifera*, the Dwarf Cavendish banana, *Chrysanthemum morifolium*, *Opuntia cylindrica*, *Bellis perennis*, *Xanthium pennsylvanicum* and *Liriodendron tulipifera*.

The cambium-like transitional zone is always associated with leaf primordia. In *Ficus carica*, for example, a series of such zones can be seen in a median longitudinal section of a vegetative bud. Here each cambium-like transitional zone corresponds to the basal part of the developing internode and, as such, may represent a region of more intense intercalary growth. Therefore the cambium-like transitional zone should not be used as a criterion on which shoot apices can be classified into different types.

The cells of the flank meristem are usually derived from the initials of the corpus, but in some plants they arise also from the tunica initials.

The rib meristem usually consists of cells arranged in rows which narrow towards the apex but they may sometimes be irregularly arranged. The majority of divisions in this zone are horizontal, but diagonal divisions also occur. Series of cells that increase in size as they become further distant from the central mother cells can be distinguished. With the increased cell size the vacuoles also enlarge.

From what is known today, it can be concluded that the epidermis and its derivatives originate from the outermost layer of the tunica. The flank meristem contributes to the development of the leaf primordia, the cortex, all or part of the procambium, and sometimes also the outer region of the pith.

REGIONS OF ACTIVITY IN THE APICAL MERISTEM

From the point of view of activity (cell division) two zones, which are parallel to the cyto-histological zones, are generally distinguished: (a) a central apical zone which includes the initials of the tunica and of the corpus and in which division is considered to occur rarely; and (b) a peripheral zone to which much mitotic activity is ascribed.

Extreme views as to the activity of these two zones are held by Plantefol (1947, 1948) and Buvat (1952) who, contrary to most investigators do not regard the central apical zone as having the role of cell-producing cells during the vegetative development of the plant (Fig. 27, no. 7), but as being active only when the vegetative apex becomes reproductive. They base their views mainly on the fact that in vegetative apices no divisions are found in this region. Thus, according to the above authors an inactive region *(méristème d'attente)* is present in the shoot apex.

However, Dermen (1945, 1947, 1948, 1951), by the production of periclinal polyploid cytochimeras with the use of colchicine, showed that divisions do occur in the zone of these initials. From histological investigations made on apical meristems of many species, (Millington and Fisk, 1956; Popham, 1958; Fahn *et al.*, 1963), cell divisions in the zone of the central

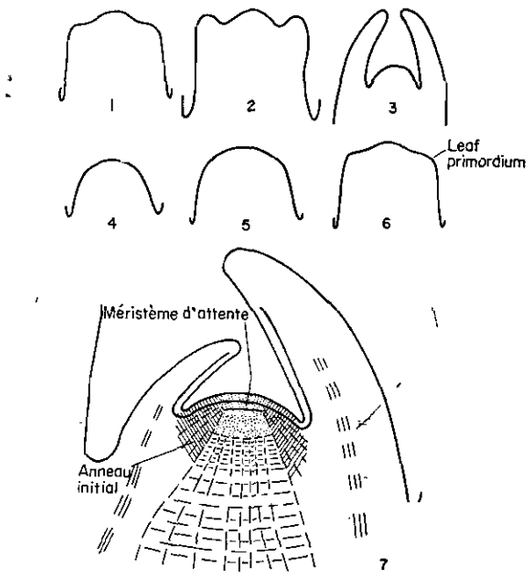

FIG. 27. 1–6, Diagrams of longitudinal sections of a shoot apex with opposite leaves showing the changes in shape and size of the apex during a plastochron. In nos. 1 and 6 the area of the apex is minimal, while in no. 5 it is maximal. 7, Diagram of the vegetative shoot apex after Buvat, showing the central inactive region *(méristème d'attente)* and a peripheral zone of high mitotic activity *(anneau initial)*.

mother cells were demonstrated. With the use of microphotographs taken with a cine camera of the surfaces of culture-grown shoot apices of several plants, Ball (1960) came to the conclusion that all the cells in the surface layer, including those at the summit of the apex, divide and do so quite frequently. Also the application of radioactively-labelled precursors of DNA (Partanen and Gifford, 1958; Gifford and Tepper, 1962a, b) did not reveal the existence of an inactive zone in the shoot apex.

Branching of the shoot originates at the shoot apex. In many pteridophytes the branching is brought about by the equal division into two of the single apical cell or group of apical cells. The resultant type of branch-

ing is termed *dichotomous branching*. In other pteridophytes and in spermatophytes, lateral buds, from which branches may develop later, are initiated in the axils of the leaf primordia.

REPRODUCTIVE APEX

The reproductive apex, which produces the flowers and bracts (Fig. 19, no. 4; Fig. 20, nos. 1–4), usually develops from a vegetative apex, which produces leaves and axillary buds. As stated by Philipson (1947, 1949), the basic function of the vegetative apex is to promote longitudinal growth of the axis and that of the reproductive apex is to produce a meristematic envelope with large surface area from which the parts of a flower or flowers develop. This meristematic envelope is superimposed on a base of parenchymatous tissue. Many investigators (Boke, 1947; Popham and Chan, 1952; Wetmore *et al.*, 1959; Fahn *et al.*, 1963, and others) have shown that the transition from vegetative to reproductive apex is gradual. The first noticeable change is the increase of mitotic activity on the boundary between the central mother cell zone and the rib meristem zone. Gradually this activity spreads into the central mother cell zone where the cells then become smaller and richer in protoplasm. In this way all the cells above the rib meristem are added to the tunica, the cells of which are more or less isodiametric and are relatively small. Following these changes mitotic activity and growth ceases, or almost so, in the cells of the rib meristem and of the pith below it. Thus, in the apex a parenchymatous pith surrounded by meristematic cells develops (Fig. 28, no. 1). Depending on the species, the bracts, the axillary branches of the inflorescence and the flowers themselves develop from these meristematic cells. An apex in this stage of development ceases to elongate in plants with capitula or single flowers, and in other plants the rate of elongation is reduced. In certain plants, such as banana, for example, an extensive and rapid elongation takes place. In such apices a well-developed rib meristem can be observed, and this meristem probably participates in the process of elongation.

These histological changes are no doubt accompanied by physiological and biochemical changes. This may be demonstrated by the fact that the dominance of the main apex, which suppresses the development of the lateral buds, is lost with the production of the inflorescence.

THE ROOT APEX

In the embryo, within the seed, only the promeristem of the root or, sometimes, an embryonic radicle may be seen at the base of the hypocotyl. Only after the germination of the seed and with the development of the

primary root can any definite arrangement be discerned in the promeristem. The promeristem of the lateral and adventitious roots have a similar structure to that of the primary root. The structure of the root promeristem has been intensively studied in order to discover the origin of the various tissues.

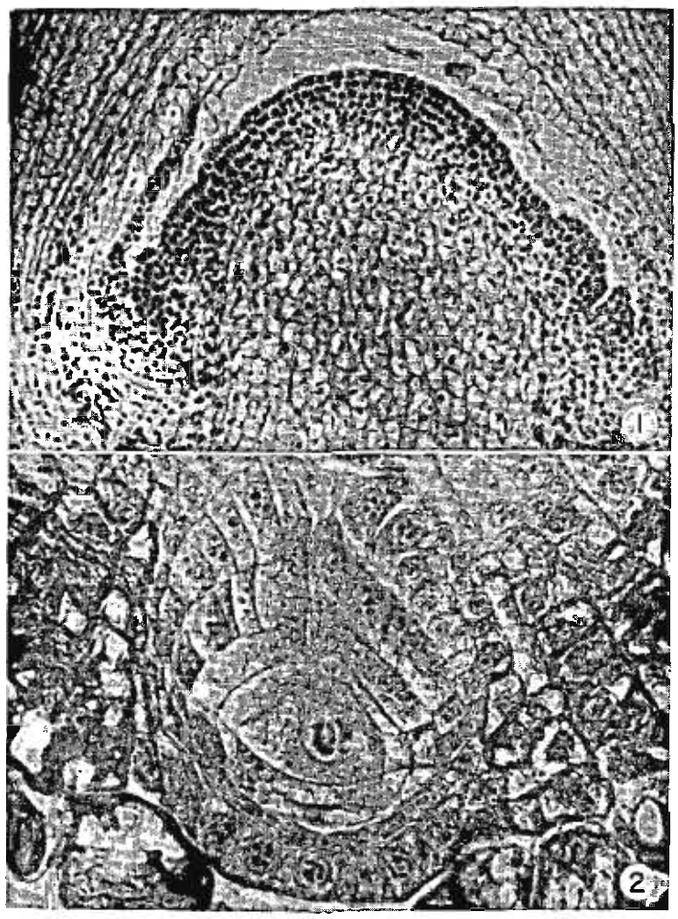

FIG. 28. 1, Micrograph of a longitudinal section of a reproductive shoot apex of *Chrysanthemum anethifolium* at an early stage of development. ×160. 2, Micrograph of a longitudinal section of a developing root of *Marsilea* in which it is possible to distinguish a single apical cell which contributes cells both towards the body of the root (upper side of micrograph) and towards the root cap (lower side of micrograph). ×600.

In some of the Pteridophyta, as, for instance, the Polypodiaceae, Ophioglossaceae and *Equisetum*, the entire root develops from a single apical cell (Fig. 28, no. 2; Fig. 29, no. 1), while in others, e.g. the Marattiaceae, a few initials are present. When there is only a single apical cell it is tetrahedral, and it divides in such a way so as to add new cells to the body of the root from its upper three sides and to the root cap from its base.

According to various investigators (Guttenberg, 1940, 1947, 1960; Schade and Guttenberg, 1951; Guttenberg *et al.*, 1955) it appears that

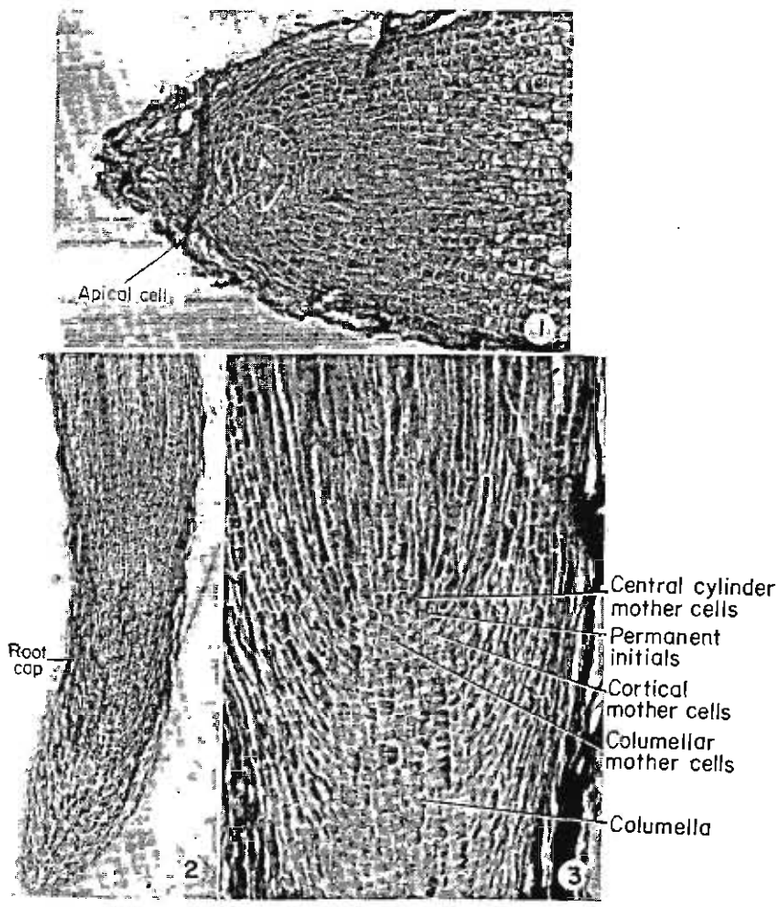

FIG. 29. 1, Micrograph of a longitudinal section of the root tip of *Ophioglossum lusitanicum* in which a single apical cell can be distinguished. ×95. 2, Longitudinal section of the root tip of *Pinus pinea*. ×30. 3, Portion of no. 2 enlarged. ×100.

there is a single central initial or but a few initials in the root apex of the Spermatophyta (Fig. 30, no. 3; Fig. 31, no. 1). Other investigators, however, such as Clowes (1950, 1953, 1954, 1961), believe that there is a larger group of initials in the median region of the root apex.

Allen (1947), working on *Pseudotsuga* (Fig. 30, nos. 1, 2), distinguished a central group of permanent initials with three groups of temporary ini-

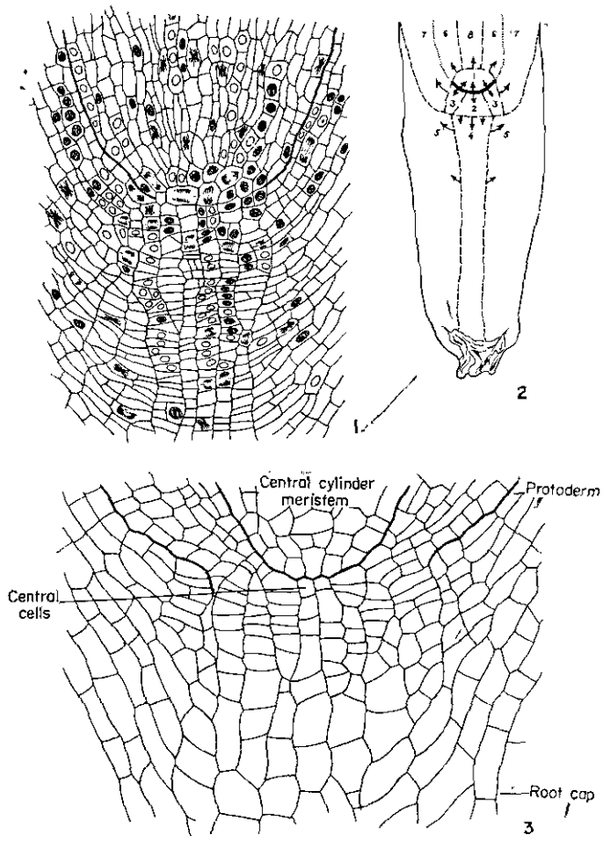

FIG. 30: 1 and 2, Median longitudinal sections of a root of a *Pseudotsuga* seedling. 1, Camera lucida drawing in which it is possible to trace the divisions in the permanent initials. × 140. 2, Diagram of entire root tip in which the zone of permanent initials is indicated by a thick line; (1) temporary initials from which the central cylinder, (6) and (8), develops; (2) temporary initials which give rise to the columella (4) from which the root cap (5) develops as a result of lateral divisions; (3) temporary initials of the cortex (7) from which the protoderm develops. 3, Longitudinal section of a young root tip of *Helianthus annuus*. (Nos. 1 and 2, adapted from Allen, 1947; no. 3, adapted from Guttenberg *et al.*, 1955.)

tials (mother cells) on its periphery. He observed that the meristem of the vascular cylinder developed from the first group of temporary initials, the meristem of the cortex from the second, and the *columella* from the third. The columella is a group of cells that forms the longitudinal axis of the root cap. In it the cells are arranged in longitudinal rows. Cells are added to the root cap from the columella by periclinal cell division on its periphery. The protoderm was seen to develop from the young cortex. According to Wilcox's work on *Abies procera* (1954) there appear to be two groups of temporary initials, one of which gives rise to the central cylinder and the other to the columella, from which the root cap and cortex develop.

Although research on the development of the histogens in the shoot apex has proved that they do not exist, many authors still use the terms *dermatogen*—meristem of the epidermis, *periblem*—meristem of the cortex, and *plerome*—meristem of the central cylinder, in connection with roots. However, the terms, as used today, have a somewhat different meaning to those as used by Hanstein. The mother cells of the various tissue systems of the root are replaced, at relatively long intervals, by new cells which are derived from the common permanent initials. In many cases more than one tissue develops from a group of mother cells (temporary initials) and so it is desirable to use, wherever possible, instead of histogens, the terms *protoderm, meristem of the cortex* and *meristem of the vascular cylinder* for the meristems that are derived from the *promeristem*, i.e. from the zone of permanent and temporary initials of the root apex.

Adapting Guttenberg's view the meristems of the different tissue systems can be traced, in the root apex, at various distances from the central cells (i.e. the permanent initials). In some species the initials (temporary) of the various tissue systems are already discrete immediately adjacent to the central cells, i.e. *closed type*. These initials represent those of the vascular cylinder, the cortex and the common initials of the protoderm and root cap, e.g. as in *Brassica*, or the separate initials of the protoderm and the root cap, e.g. as in *Zea* and *Triticum* (Fig. 31, no. 1). The special initials of the root cap were termed *calyptrogen* by Janczewski (1874). In other species the meristems of the different tissue systems finally become distinct only some distance away from the central cells, i.e. *open type*. In this type common initials for the cortex meristem, root cap and protoderm (e.g. *Helianthus*, Fig. 30, no. 3) or for the meristems of all the tissue systems (e.g. *Allium*) appear on the periphery of the central cells. The importance of the above types is queried as they have been observed to occur in the roots of a single species.

Recent research (Jensen, 1957; Clowes, 1958 a, b, 1961; Jensen and Kavaljian, 1958) on the promeristem of the root apex has shown that the cells of the central part of the promeristem have very low mitotic activity. This part is termed *quiescent centre* (Fig. 31, no. 2).

It is also necessary to mention here the *Körper–Kappe theory* (Fig. 31,

no. 3) which was put forward by Schüepp (1917). This theory, similar to the tunica–corpus theory of the shoot apex, is based on differences in the planes of cell division. According to the Körper–Kappe theory the cells

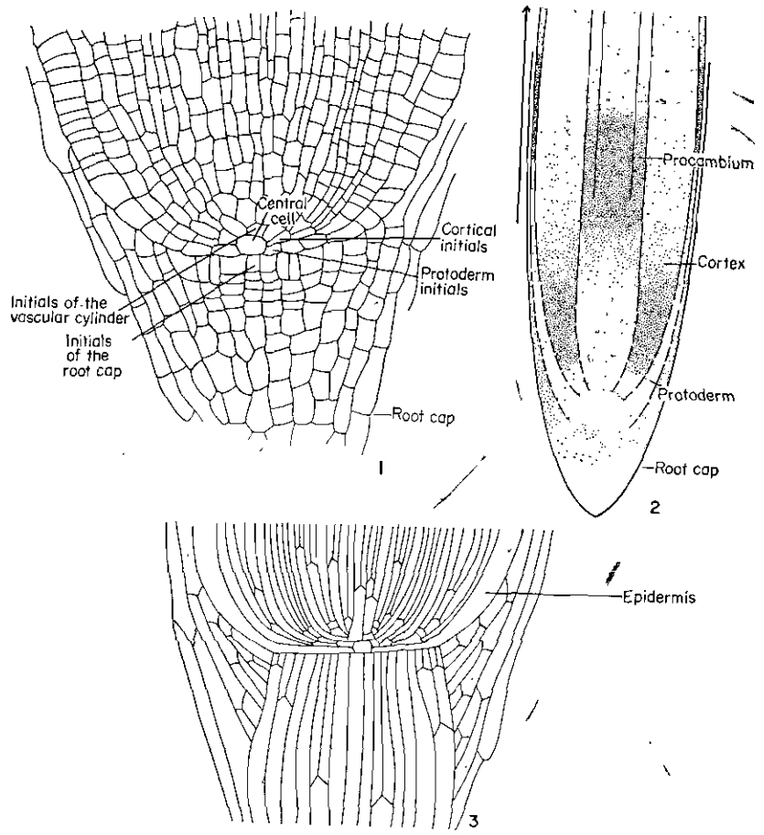

FIG. 31. 1, Longitudinal section of the root tip of *Triticum vulgare*. 2, Diagram of the root tip of *Allium cepa* showing, by means of shading, the gradation of mitotic activity in different zones; the most active zone is the most darkly shaded. 3, Diagram illustrating the Körper–Kappe pattern of the root apex of *Zea mays*. (No. 1, adapted from Schade and Guttenberg, 1951; no. 2, adapted from Jensen and Kavaljian, 1958; no. 3, adapted from Clowes, 1961.)

divide in a pattern which was termed T-divisions. In the outer regions fo the root apex the Kappe consists of cells in which, after the first horizontal division, the lower daughter cell divides longitudinally, i.e. at right-angles to the plane of the first division. Thus the planes of the two divisions form

a "T" in a median longitudinal section of the root. In the Körper—the inner region of the apex—the "T" is inverted, i.e. the second division takes place in the upper daughter cell. In some families, such as the Gramineae, the position of the boundary between these two regions was found to be constant in relation to the meristems of the various tissue systems, but in other plants, e.g. *Fagus*, the boundary may occur in different positions in the root tip, such as in the middle of the cortex, between the cortex and the epidermis, etc. (Clowes, 1961). Körper-type T-divisions can also be seen in the central column of the root cap in *Fagus*.

Intercalary meristems

Intercalary meristems are parts of the apical meristem that become separated from the apex during the growth of the plant by regions of more mature tissues (Fig. 24, no. 1). In stems with intercalary meristems the nodes mature earlier and the intercalary meristems are localized in the internodes. At first, the entire internode is meristematic, but with further development part of the internode matures faster and so various stages of development can be found in the internode. In most plants with intercalary meristems the region with the cells showing the least degree of differentiation is at the base of the internode, but this region may sometimes be found in the middle or at the top of the internode (Eames and MacDaniels, 1947). In more mature stages the intercalary meristems are separated from each other by fully matured tissues and they, themselves, are penetrated by vascular bundles that consist of protoxylem and protophloem. Finally, the intercalary meristems undergo complete differentiation and so disappear.

The best-known examples of intercalary meristems are those in the stems of grasses, some other monocotyledons, some species of the Caryophyllaceae, and articulated species of the Chenopodiaceae and *Equisetum*. Intercalary meristems also occur in the peduncles of the inflorescences of certain plants, in the leaves of many monocotyledons (e.g. in the Gramineae and *Iris*), Pinaceae and others. The gynophore of *Arachis* (ground nut) also elongates as a result of the activity of an intercalary meristem (Jacobs, 1947).

Internodal elongation in many grasses is brought about by an intercalary meristem, the cells of which divide to form parallel series of cells and which is, therefore, termed rib meristem (not to be confused with the rib meristem of apices). The enlargement of the derivatives of this meristem also contributes to the elongation of the internode (Miltényi, 1931; Kaufman, 1959). Miltényi states that the intercalary meristems of grass internodes have no fixed position, but that their position is altered as the internode elongates. At first the intercalary meristematic activity occurs throughout

the internode, as has already been mentioned above; but after the development of the lacunae, that are present in most grasses, this activity becomes restricted to the peripheral ground tissue in the proximity of and above the nodal plate, i.e. in the joint regions. The meristematic activity of the joints can be reactivated even in mature stems. It has been shown that, in those parts of plants that have already undergone a certain degree of differentiation, such as in flowers, fruits, leaves and stems without special intercalary meristems, the cells continue to divide for a long time after they have been derived from the apical meristem. This type of growth can also be considered as intercalary, but the growth regions are less well defined.

In the last 30 years many investigators have been attracted to research on meristems, and especially on apical meristems. This interest is due to the great importance of the apex in which the pattern of initiation of leaves, buds, flowers and the various tissues is determined. The continuity of the tissue systems of the shoot and root result from the activity of the apices. Because the systems of essential elements, such as the tracheary elements, cannot undergo further changes once they are fully differentiated, and because they must be stable and continuous in order to function, the structure of the plant must be determined in the apical meristem. In long-lived plants with secondary thickening, the continuity of the conducting systems between the young parts of the root and shoot is brought about by secondary vascular tissues which are produced by the vascular cambium, a lateral meristem.

The problem of the indentification of initials has been solved for shoot apices of the lower vascular plants, with a single apical initial. In higher vascular plants the exact delimitation of the initials in the apex is still unsettled. In the root apex, for instance, changes in the size of the quiescent centre have been observed (Clowes, 1961). This phenomenon is certainly correlated with changes occurring in the initials. These changes suggest that the mother cells of the various tissue systems of the root, situated on the periphery of the quiescent centre, are not permanent initials. These initials become further distant from the quiescent centre and then their former position is taken up by new initials which must, therefore, be produced in the quiescent centre in which the permanent initials are found. The exact location of the various types of initials in the shoot apex of most spermatophytes is even more difficult than in the root tip, as in the shoot apices, contrary to the root tip, all the apical cells divide fairly frequently.

The permanent initials of the root, which exhibit very low mitotic activity, may, as already suggested by Clowes (1961), function as sites of hormone synthesis and in the maintenance of the geometry of the apical meristem.

In conclusion, from the data on apices accumulated until now, we have to realize that we do not, as yet, know the exact pattern of initiation and differentiation in the apical meristems. Still less clear is the physiological interpretation of apical morphogenesis.

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MATURE TISSUES

IT IS the usual practice to divide the plant body into different tissues, but with the accumulation of knowledge of tissue structure it becomes more and more difficult to give an exact definition of a tissue. The accepted definition of a tissue is a group of cells with common origin, structure and function. However, this definition is not suitable for all cases. When dealing with the tissues of higher plants a more flexible definition is necessary. If we could base our descriptions on elements, i.e. the individual types of cells, it would be easier to define these units. However, difficulties would also arise from such a classification because of the transitional forms present. For the sake of convenience, in this book the anatomical and histological structure of plants will be discussed on the basis of tissue classification. Today a complex of cells of common origin is generally understood by the term tissue. A tissue may consist of cells of different form and even different function, but in tissues consisting of different cell types the cell composition is always the same.

The tissues in the plant body are classified on the following bases: according to their position in the plant; the cell types of which they consist; their function; the manner and place of their origin; and their stage of development. Tissues are also divided into *simple* and *complex tissues* according to the number of cell types that they comprise. A simple tissue is homogeneous and consists of only one type of cell, while a complex tissue is heterogeneous and comprises two or more cell types. *Parenchyma, collenchyma, sclerenchyma* and *laticifers* are examples of simple tissues. All other tissues are complex. Complex tissues, however, may contain parenchyma, sclerenchyma or other elements. Examples of complex tissues are *xylem* and *phloem*.

CHAPTER 4

PARENCHYMA

THE parenchyma of the primary plant body develops from the ground meristem, and that connected with the vascular elements, from the procambium or cambium. The phellogen in many plants also produces parenchyma (the phelloderm). Parenchyma consists of living cells of differing shape and with differing physiological functions.

By the term parenchyma we generally refer to tissues which exhibit relatively little specialization, and which may be concerned with various physiological functions of the plant.

Parenchyma cells retain the ability to divide even when mature. They also play an important role in wound recovery and regeneration. Phylogenetically the parenchyma of the primary body is considered to be a primitive tissue as the lowest multicellular plants consist of parenchyma only. Ontogenetically parenchyma may also be considered primitive as its cells are morphologically similar to those of meristems.

Large portions of the plant, such as the pith, all or most of the cortex of the root and shoot, the pericycle, the mesophyll of the leaf and the fleshy parts of fruits, consist of parenchyma. Parenchyma cells also occur in the xylem and phloem.

SHAPE AND ARRANGEMENT OF PARENCHYMA CELLS

Many parenchyma cells are polyhedral and their diameter in the different planes is more or less equal (Fig. 33, no. 1) but many other shapes are common. Elongated parenchyma cells are found in the palisade tissue of the leaf, in the medullary rays, etc.; lobed cells are found in spongy mesophyll and in the palisade parenchyma of *Lilium* (Fig. 89, no. 1); and in the mesophyll of the Xanthorrhoeaceae the parenchyma cells have folds or projections (Fahn, 1954). Stellate parenchyma cells are found in the stems of plants with well developed air spaces, such as *Scirpus* and *Juncus*, for example (Fig. 32, no. 1). In *Juncus*, according to Geesteranus (1941), the stellate pith cells differentiate ontogenetically from a mass of cubo-octahedral cells which are arranged in vertical rows on their hexagonal faces. The mechanical stretching of the pith, which is mainly in a radial direction as a result of the growth of the surrounding tissues, as well as the special arrangement of the intercellular spaces, causes the development of the characteristic arms of the cells.

The medium-sized polyhedral parenchyma cells usually have fourteen faces (Higinbotham, 1942; Lewis, 1944; Matzke, 1946; Hulbary, 1948); the number of sides is less in the smaller cells and greater in the larger cells (Marvin, 1944). The number and size of the intercellular spaces also affects the number of faces of the polyhedron as the presence of intercellular spaces reduces the planes of contact between the cells. The polyhedral shape of the parenchyma cells is the result of numerous factors among which are pressure and surface tension (see Chapter 2).

Mature parenchymatous tissue may be tightly packed and without intercellular spaces or it may have a well developed system of intercellular spaces. For example, the parenchyma of the endosperm of most seeds is devoid, or almost so, of intercellular spaces, while in the stems and leaves of hydrophytes the intercellular spaces reach maximal development.

The development of intercellular spaces is either *schizogenous* or *lysigenous*. The schizogenous development of an intercellular space takes place as follows: at the time when the primary wall is formed between two new cells the middle lamella between the two new cell walls (Fig. 9, nos.

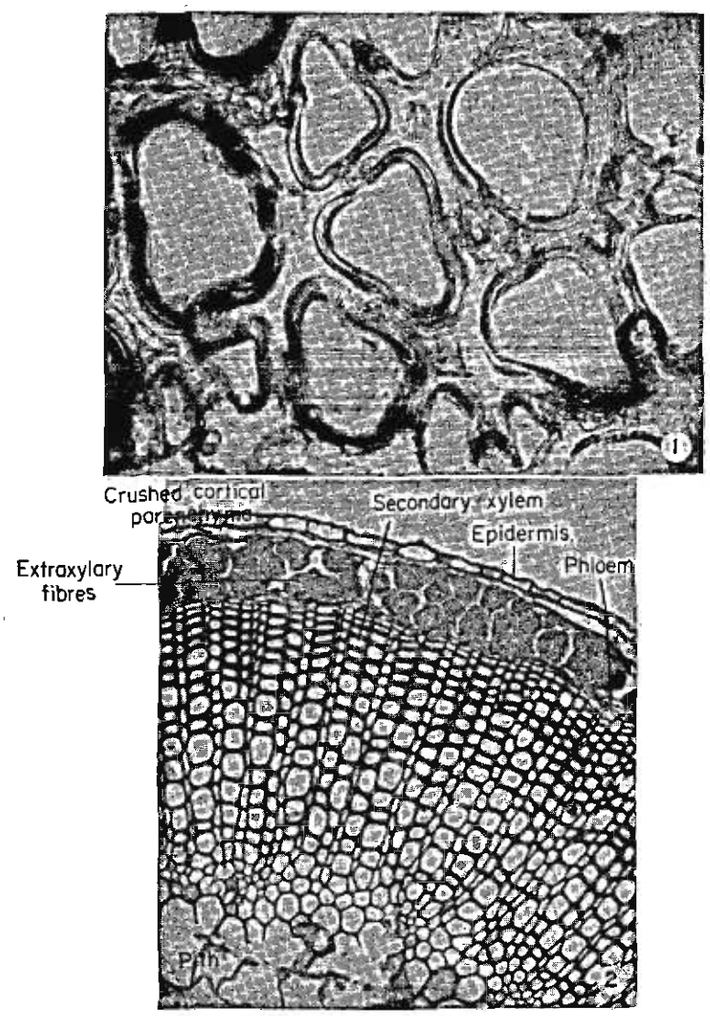

FIG. 32. 1, Micrograph of stellate parenchyma cells as seen in a cross-section of the stem of *Cyperus papyrus*. ×430. 2, Micrograph of portion of a cross-section of *Linum usitatissimum* in which the extraxylary fibres can be distinguished ×115.

7–10) comes into contact only with the primary wall of the mother cell and not with the middle lamella between it and the neighbouring cells. Thus, a small space develops where the new middle lamella comes into contact with the mother cell wall. That portion of the mother cell wall opposite this small space disintegrates and so forms the intercellular space which can be enlarged by the formation of a similar space in the neighbouring

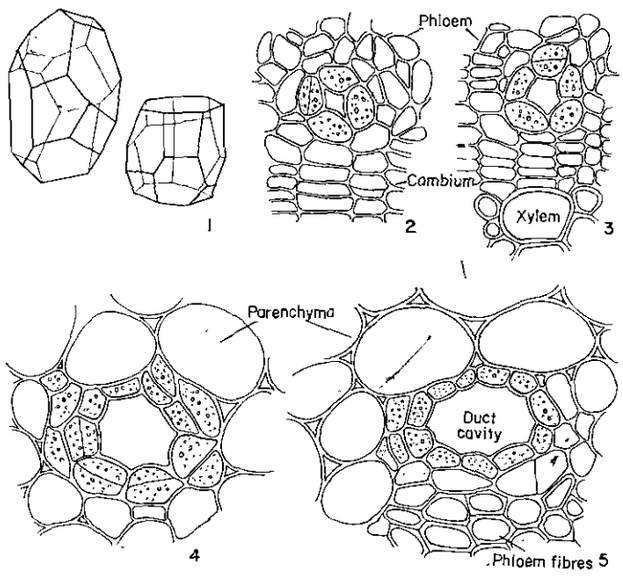

FIG. 33. 1, Polyhedral parenchyma cells. 2–5, Portions of cross-sections of the stem of *Hedera helix* showing different stages in the schizogenous development of a secretory duct. (No. 1, adapted from Marvin, 1944; nos. 2–5, adapted from Palladin, 1914.)

cell. The intercellular space is lined with the substance of the middle lamella. These intercellular spaces may be further enlarged by divisions of the surrounding cells in a plane perpendicular to the circumference of the space. The resin ducts of the Coniferae, the secretory ducts of the Compositae, Umbelliferae, *Hedera helix* (Fig. 33, nos. 2–5) and other species, are formed schizogenously. Lysigenous intercellular spaces are formed by the disintegration of entire cells. Examples of lysigenous intercellular spaces are the large spaces in water plants and in the roots of some monocotyledons, and also the essential oil cavities in *Eucalyptus*, *Citrus* (Fig. 34, nos. 1–6) and *Gossypium*.

STRUCTURE AND CONTENT OF PARENCHYMA CELLS

Most parenchyma cells, e.g. those that contain chloroplasts and those that act as storage cells, usually have thin primary walls, but parenchyma cells with thick primary walls also exist. Certain parenchyma storage cells, as, for example, the endosperm of *Phoenix* (Fig. 212, no. 3), *Diospyros*, *Coffea* and *Asparagus*, have very thick walls in which hemicellulose, which

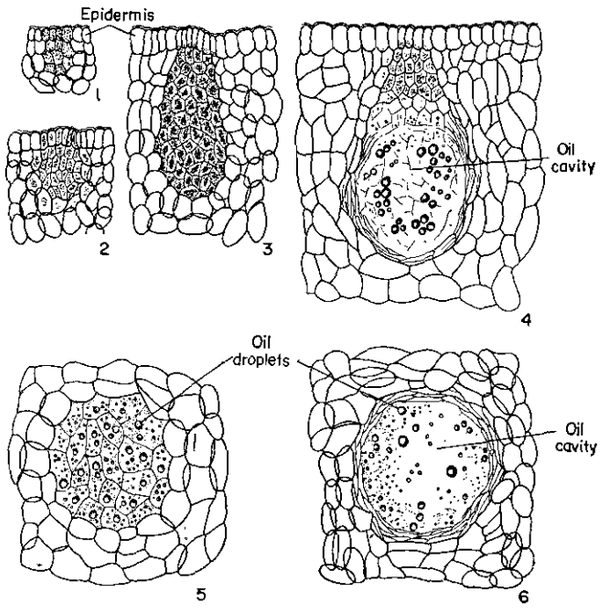

FIG. 34. Lysigenous development of an essential oil cavity in the peel of the fruit of *Citrus*. 1–4, Sections at right-angles to the surface of the peel. 5 and 6, Sections parallel to the surface of the peel. (Adapted from Martinet, 1871.)

serves as the reserve substance, accumulates. The walls of these cells gradually become thinner during germination. Parenchyma cells with relatively thick and lignified secondary walls are common, especially in the secondary xylem.

The internal structure of the parenchyma cell varies according to its function. Parenchyma cells which take part in photosynthesis contain chloroplasts and then the tissue they form is termed *chlorenchyma*. In the photosynthetic parenchyma there are usually many or large vacuoles. Certain parenchyma cells contain leucoplasts. Parenchyma cells may serve to store different reserve materials which may be found in solution in the vacuoles, or in the form of solid particles or liquid in the cytoplasm. Sugars

or other soluble carbohydrates and nitrogenous substances may be found in the cell sap. Amides, proteins and sugars are found dissolved in the cell sap, as, for example, in the roots of the sugar beet and in the bulb scales of *Allium cepa*. Starch, protein, oils and fats occur in the cytoplasm in the form of small particles. Protein and starch grains are found in the cytoplasm of the cells of the cotyledons of many species of the Leguminosae, and protein and oils are found in the endosperm of *Ricinus communis* and the cotyledons of *Glycine max*. In the parenchyma cells of the potato tuber, for example, amides and proteins are found in the cell sap and starch in the cytoplasm. Starch is the most common reserve material in plants and it is found in the endosperm, cotyledons, tubers, fruits, xylem and phloem parenchyma, the cortex, etc.

In succulent plants parenchyma cells that store water are present. Such cells are usually large, thin-walled and have only a thin layer of cytoplasm, and they are devoid of, or contain very few, chloroplasts. The water-storing cells have a large vacuole which contains somewhat mucilaginous sap. The mucilaginous substances apparently increase the water-holding capacity of the cell, and they are also present in the cytoplasm and wall.

The parenchyma cells of different storage organs contain water as well as reserve substances, as, for instance, in the potato tuber which supplies water to the developing parts of the plant at the start of the sprouting process.

Many parenchyma cells contain tannins, and such cells may be scattered throughout the plant or they may form continuous systems. Most of the tannins are found in the vacuoles. Tannin-containing cells retain the ability to divide and grow as do parenchyma cells devoid of tannins. Mineral substances can be found in various crystalline forms in parenchyma cells. Some such cells may remain viable after the formation of the crystals but others die.

Idioblastic parenchyma cells may contain various substances such as the enzyme myrosin (Cruciferae, Capparidaceae, Resedaceae, etc.), oily substances (Lauraceae, Simarubaceae, Calycanthaceae, etc.), mucilaginous substances (many monocotyledons and the Cactaceae, Portulacaceae, Malvaceae, Tiliaceae, etc.) and resiniferous substances (Meliaceae, some Rutaceae, Rubiaceae, etc.) (Sperlich, 1939; Metcalfe and Chalk, 1950).

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CHAPTER 5

COLLENCHYMA

THE supporting tissues of the plant, i.e. the collenchyma and the sclerenchyma, are designated from the functional point of view by the term *stereome* (Haberlandt, 1918).

Ontogenetically collenchyma develops from elongated cells which resemble procambium and which appear in the very early stages of the differentiation of the meristem. Collenchyma consists of living, slightly elongated cells which, generally, have unevenly thickened walls. Collenchyma functions as a supporting tissue in young growing organs and, in herbaceous plants, even in mature organs (Ambronn, 1881; Müller, 1890; Anderson, 1927; Esau, 1936). Collenchyma is plastic and it stretches irreversibly with the growth of the organ in which it occurs. Mature collenchyma is less plastic, harder and more brittle than young collenchyma. There is a physiological and morphological relationship between collenchyma and parenchyma and, in places where the two tissues occur side by side, transitional forms can be found between typical collenchyma and typical parenchyma.

Collenchyma, like parenchyma, may contain chloroplasts. Chloroplasts occur in larger numbers in less specialized collenchyma cells which resemble parenchyma and in smaller numbers, or not at all, in the most specialized collenchyma, which consists of elongated narrow cells. Collenchyma cells may also contain tannins.

In a freshly made cross-section of collenchyma the cell walls appear *nacré*-like. It has been seen in plants exposed to wind that the walls of collenchyma cells become thicker. Collenchyma may become lignified and the walls may thicken thus resulting in the formation of sclerenchyma. The thickened walls of the collenchyma may, secondarily, become thin and then the cells may again become meristematic and start to divide as, for instance, where the phellogen is formed in collenchyma tissue. Primary pit fields can be distinguished in the walls of collenchyma cells.

Position of Collenchyma in the Plant

Collenchyma may occur in stems, leaves, floral parts, fruits and roots. In the latter collenchyma is mainly developed when they are exposed to light (Van Fleet, 1950). Collenchyma is absent in the stems and leaves of

many monocotyledons where sclerenchyma develops at an early age. Collenchyma usually forms immediately below the epidermis but, in certain cases, one or two layers of parenchyma occur between the collenchyma and the epidermis. When the collenchyma is found directly beneath the epidermis, the inner walls, or sometimes the entire wall, of the epidermal cells become thickened similarly to the walls of the collenchyma cells. In stems the collenchyma may occur as a complete cylinder or in longitudinal strips. In leaves the collenchyma occurs on one or both sides of the veins and along the margins of the blade. In many plants groups of elongated parenchyma cells which become collenchyma-like occur on the outside of the phloem strands and also on the inside of the xylem, or even as a sheath around the entire vascular bundle. When these groups are only on the sides of the xylem or phloem they appear dome-shaped in cross-section (Fig. 70, no. 2).

Structure and Arrangement of Collenchyma Cells

The size and shape of the collenchyma cells varies. The cells may be short prisms and resemble the neighbouring parenchyma cells, or long and fibre-like with tapered ends, but all intermediate shapes and sizes occur. The longest collenchyma cells are found in the central portions of the strands of collenchyma, and the shorter ones on the periphery. This can be explained as follows: the collenchyma strands are formed by a series of longitudinal divisions which start in the centre of the strand; the cells continue to elongate after division and therefore the central cells are the longest as they are the first to be formed and to reach the maximum length. During the development of the collenchyma strands horizontal divisions also take place.

According to the type of wall thickening two main types of collenchyma can be distinguished.

1. *Angular collenchyma* (Fig. 35, no. 1) in which the thickening of the cell wall is longitudinal in the angles of the cells. In cross-section these thickenings are seen to be in those places where three and more cells meet. Examples of such collenchyma are found in the petioles of the leaves of *Vitis*, *Begonia*, *Coleus*, *Cucurbita*, *Morus*, *Beta*, and in the stems of *Solanum tuberosum*, *Atropa belladonna* and *Nicotiana tabacum*.

2. *Lamellar collenchyma* (Fig. 35, no. 2) in which the thickenings are mainly on the tangential walls of the cells. Examples of this type of collenchyma are found in the stem cortex of *Sambucus nigra* and the petiole of *Cochlearia armoracia*.

Some authors distinguish a further type, i.e. lacunar collenchyma (Foster, 1950), and others yet another type, i.e. annular collenchyma (Duchaigne, 1955). The lacunar type is described as that in which the thickening

appears in those parts of the cell wall that face intercellular spaces. Such collenchyma can be seen in the petioles of species of the Compositae, *Salvia*, *Malva*, *Althaea* and *Asclepias*. However, as intercellular spaces can be distinguished in other types of collenchyma, this does not seem to be a valid criterion for the classification of a special type. Annular collenchyma (Fig. 35, no. 3) is described as being collenchyma in which the

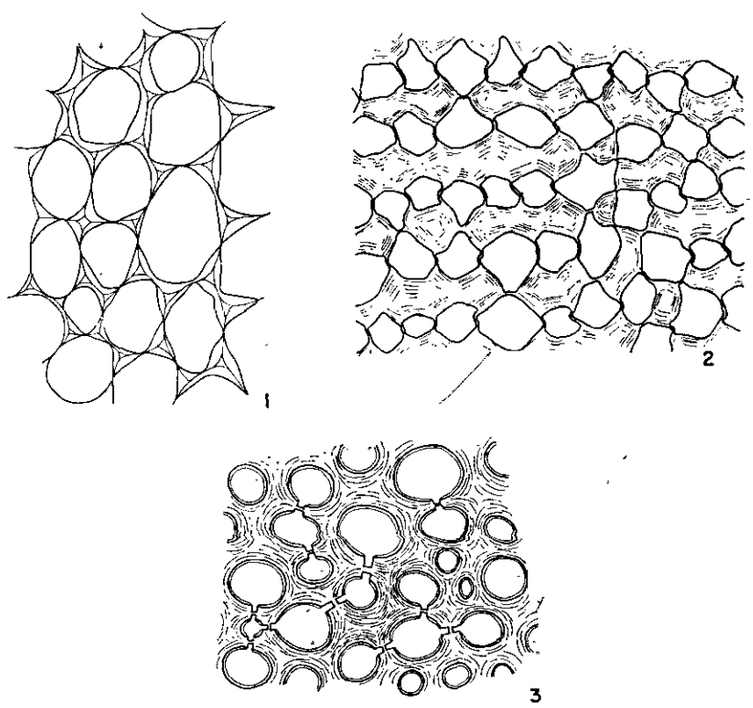

FIG. 35. Different types of collenchyma. 1, Angular collenchyma as seen in a cross-section of the stem of *Nicotiana tabacum*. 2, Lamellar collenchyma as seen in a cross-section of the cortex of a young branch of *Sambucus*. 3, Annular collenchyma as seen in cross-section of the main vein of a leaf of *Nerium oleander*.

cell lumen is circular, or almost so, in cross-section. However, from observations made on the maturation of angular collenchyma, it was seen that, with the continued thickening of the cell wall, the lumen loses its angular appearance.

The walls of collenchyma cells consist of alternating layers that are rich in cellulose and poor in pectic compounds and those which are poor

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in cellulose and rich in pectic compounds. In fresh material the water content of the entire wall is about 67%. Roelofsen (1959) states that in *Petasites* the collenchyma cell walls contain 45% pectin, 35% hemicellulose and about 20% cellulose. Preston and Duckworth (1946) and Majumdar and Preston (1941), working on *Petasites* and *Heracleum*, found that the walls of collenchyma cells, or at least the angular thickenings, consisted of seven to twenty lamellae which were alternately rich and poor in cellulose but which become richer in cellulose as they approach the cell lumen. According to some authors (Duchaigne, 1955; Beer and Setterfield, 1958), the additional layers of microfibrils that appear during the development of the characteristic wall thickenings seem to arise both on the outside and on the inside of those layers that are continuous around the entire cell. In very thick walls the additional layers extend around the cell. In this type of wall pits can be seen. Collenchyma cells are apparently the only cells in which it is not known which part of the wall is laid down during the period of longitudinal growth and which part after the cells have reached maximum length. It is, therefore, impossible to delimit the primary and secondary wall layers in these cells.

In many dicotyledons, e.g. in the petioles and stems of *Medicago sativa*, *Eryngium maritimum*, *Viscum album* and *Salvia officinalis*, the collenchyma may become sclerified. This sclerification is brought about, according to Duchaigne (1955), by a process of centripetal and centrifugal lamellation. The inner lamellae, during the process of growth, together form a layer rich in cellulose which later becomes impregnated with lignin. New concentric, lignified lamellae appear centrifugally around the first such layer. As a result of this centrifugal development of lignified lamellae, the pectocellulosic substance of the collenchyma walls progressively disappears. Often, however, part of this substance remains even after the walls become fully sclerified. Later, additional lamellae develop centripetally and so the cell lumen is gradually reduced. The greatest concentration of lignin is finally found in the outermost wall layers. Simple pits are also present here as in sclerenchyma.

Generally, we can conclude that typical collenchyma is a juvenile supporting tissue, and when it is present in an organ which persists for a long period it becomes sclerified.

The peculiar manner in which the walls of collenchyma cells become thickened, i.e. by centrifugal as well as centripetal apposition of lamellae, is a very interesting phenomenon and further research is necessary to clarify how microfibrils are produced outside the existing wall. This, probably, will also lead to a better understanding of wall growth, both in thickness and in surface area.

CHAPTER 6

SCLERENCHYMA

SCLERENCHYMA is a tissue composed of cells with thickened secondary cell walls, lignified or not, whose principal function is support and sometimes protection. Sclerenchyma cells exhibit elastic properties unlike collenchyma cells which exhibit plastic properties.

Sclerenchyma cells may differ in shape, structure, origin and development. Many transitional forms exist between the various cell shapes and thus it is difficult to classify the different types of sclerenchyma. Generally, sclerenchyma is divided into *fibres* and *sclereids*. Fibres are usually defined as long cells and sclereids as short cells. This definition is not sufficient, as very long sclereids exist and relatively short fibres can be found. Attempts to describe the differences between fibres and sclereids were made on the basis of the presence of pits which are more numerous in sclereids, as well as on the origin of the elements. Sclereids develop from parenchyma cells whose walls become secondarily thickened, whereas fibres develop from meristematic cells and so they are determined from their origin. Other research, however, has shown that these definitions are also insufficient due to their inconstancies. Not only is it difficult to distinguish between the different types of sclerenchyma cells because of the existing transitional forms, but it is also somewhat difficult to distinguish between sclerenchyma and parenchyma as there are parenchyma cells with thick secondary walls, such as the xylem parenchyma.

Fibres

Fibres occur in different parts of the plant body. They may occur singly as idioblasts (e.g. in the leaflets of *Cycas*), but more usually they form bands or a network or an uninterrupted hollow cylinder (Fig. 32, no. 2). Fibres are most commonly found among the vascular tissues but in many plants they are also well developed in the ground tissues. According to their position in the plant body, fibres are classified into two basic types—*xylary* and *extraxylary* fibres.

Xylary fibres constitute an integral part of the xylem and they develop from the same meristematic tissues as do the other xylem elements. These fibres are of varied shape in spite of their common origin. Two main types of xylary fibres, i.e. *libriform fibres* and *fibre-tracheids*, are distinguished

on the basis of wall thickness and type and amount of pits (Fig. 37, nos. 1–3). Libriform fibres resemble phloem fibres (liber=inner bark) and they are usually longer than the tracheids of the plant in which they occur. These fibres have extremely thick walls and simple pits. Fibre-tracheids are forms intermediate between tracheids and libriform fibres. Their walls are of medium thickness—not as thick as those of the libriform fibres but thicker than those of the tracheids. The pits in fibre-tracheids are bordered but their pit chambers are smaller than those of tracheids. In fibre-tracheids and sometimes also in libriform fibres the pit canal is elongated and the inner pit aperture usually becomes slit-like (Fig. 18, no. 1) as a result of the thickening of the wall. In fibre-tracheids, therefore, the length of the pit aperture usually exceeds the diameter of the pit chamber. In both libriform fibres and fibre-tracheids, the inner pit apertures of a pit-pair are usually at right-angles to each other.

Another type of fibre present in the secondary xylem of dicotyledons is the *gelatinous* or *mucilaginous fibre* (Fig. 138, no. 1). In such fibres the innermost layer of the secondary wall contains much α-cellulose and is poor in lignin. This layer, termed the "G layer", absorbs much water and may swell so as to fill the entire lumen of the fibre. On drying, these layers shrink irreversibly (Dadswell and Wardrop 1955). The G-layers were found to be relatively porous and less compact than the adjacent outer layers (Cote and Day, 1962). Gelatinous fibres are characteristic of tension wood.

Extraxylary fibres occur elsewhere in the plant other than among the xylem elements. They occur, for instance, in the cortex or they may be closely related to the phloem elements. In the stems of many monocotyledons, the extraxylary fibres occur in an uninterrupted hollow cylinder in the ground tissue, and they may be situated at various distances inside the epidermis and may even surround the outermost vascular bundles. Commonly in the monocotyledons, the fibres form sheaths around the vascular bundles. Such fibres develop partly from the procambium and partly from the ground tissue (Esau, 1943).

In the stems of climbing and certain other dicotyledonous plants, such as *Aristolochia* and *Cucurbita*, fibres are found on the inside of the innermost cortical layer and on the periphery of the central cylinder (Fig. 71). It was thought that such fibres were not developmentally connected with the phloem and so they were termed, by many workers, *pericyclic fibres*. However, Esau (1938, 1943), Blyth (1958) and others, as a result of ontogenetic studies on these fibres in many plants (*Nicotiana*, *Linum*, *Corchorus*, *Ricinus*, *Nerium*, etc.), came to the conclusion that these fibres develop from the procambium and so constitute part of the primary phloem.

The above classification into xylary and extraxylary fibres is not always applicable as there are fibres, such as the *septate fibres* (Fig. 37, no. 4), which are found in the xylem and the phloem even of the same species,

e.g. in *Vitis* where they are very common (Vestal and Vestal, 1940; Spackman and Swamy, 1949). These fibres are characterized by the presence of internal septa and, usually, of a living protoplast. The internal septa are formed by the inner lamellae of the secondary wall and middle lamellae. The latter, however, do not connect with the middle lamella of the entire fibre. Septate fibres contain starch, oils, resins and sometimes crystals of calcium oxalate and, therefore, they are thought to have a storage function.

Mature fibres have well developed, usually lignified secondary walls which are sometimes so thick as to obscure the lumen of the fibre. Lamellae can be distinguished in these walls. In *Linum*, for example, each lamella is 0·1–0·2 μ thick as seen in a cross-section of the fibre.

Mention should be made here of those elongated cells that sometimes occur in the secondary xylem and whose secondary walls are equal in thickness to those of the xylem parenchyma. These cells contain living protoplasts and, according to Haberlandt (1918), they were termed by Sanio, *substitute fibres* (*Ersatzfasern*). It appears, however, that these cells should be included among the xylem parenchyma and that they should not be confused with the living libriform fibres and fibre-tracheids (Fahn and Arnon, 1963; Fahn and Leshem, 1963) which are discussed later in this chapter.

FORM AND LENGTH OF FIBRES

Fibres are usually very long and narrow cells with tapered, and sometimes branched, ends. The length of fibres varies very greatly and generally extraxylary fibres are longer than xylary fibres. In *Cannabis sativa* (hemp) the fibres are 0·5–5·5 cm long, in *Linum usitatissimum* (flax), from 0·8 to 6·9 cm, and in *Boehmeria nivea* (ramie) Aldaba (1927) showed, by means of a special maceration, that the fibres may reach a length of 55 cm. These ramie fibres are among the longest cells in the higher plants.

DEVELOPMENT OF FIBRES

Ontogenetically fibres develop from different meristems, such as the procambium, cambium, ground meristem and even from the protoderm, as in certain species of the Gramineae and Cyperaceae. The fibres formed by the cambium develop from fusiform initials and elongate only little or not at all during their maturation.

Fibres that arise from short initials, as in *Linum* (flax) and *Boehmeria nivea* (ramie), must necessarily elongate greatly in the course of their maturation. In ramie, according to Aldaba (1927), the initials of the primary phloem fibres are 20 μ long while the mature fibres can be up to 55 cm (550,000 μ) long. The elongation is very gradual and may take some

months. This gradual elongation of primary phloem fibres involves a very complicated development of the secondary wall. While the fibre still grows symplastically, the wall remains thin. Later, when the ends begin to grow by intrusive growth, only the cell walls of the ends remain thin and secondary wall formation commences from the middle of the fibre in those parts of wall which have ceased to elongate. In *Linum* and ramie it has been

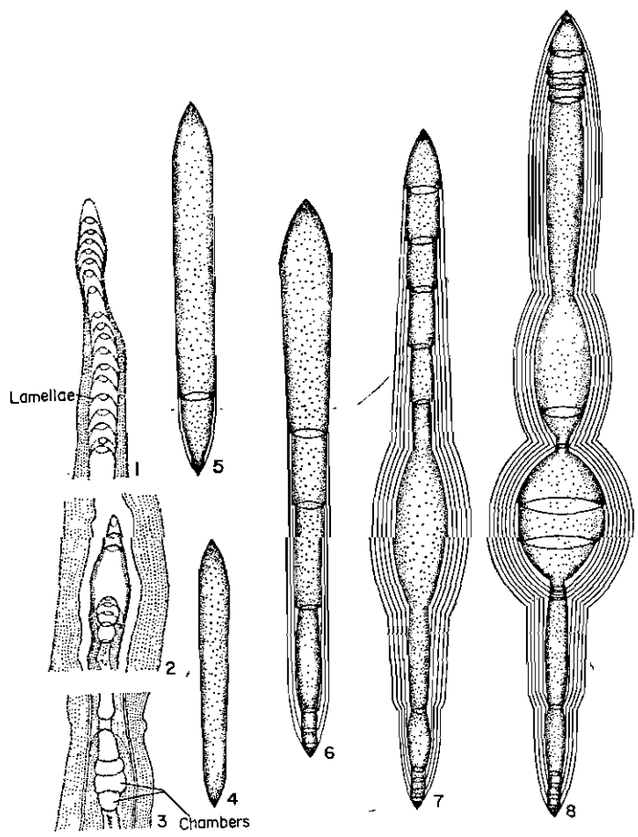


FIG. 36. Stages in the ontogeny of the extraxylary fibres of *Boehmeria nivea*. 1, Elongation of the upper end, showing a series of young lamellae one within the other; each lamella is open at its tip. 2 and 3, Development of chambers by inner lamellae. 4–8, Diagrammatic representation of the differentiation of a phloem fibre, in which the centripetal development of the lamellae of the secondary wall is shown. 8, Widened chambers, formed by the relatively increased growth of inner lamellae which are present only along part of the fibre. (Adapted from Aldaba, 1927.)

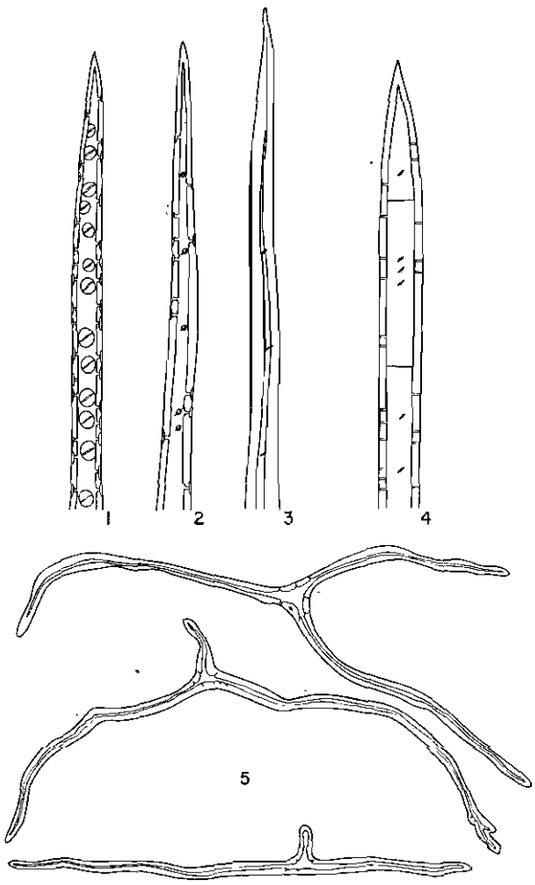
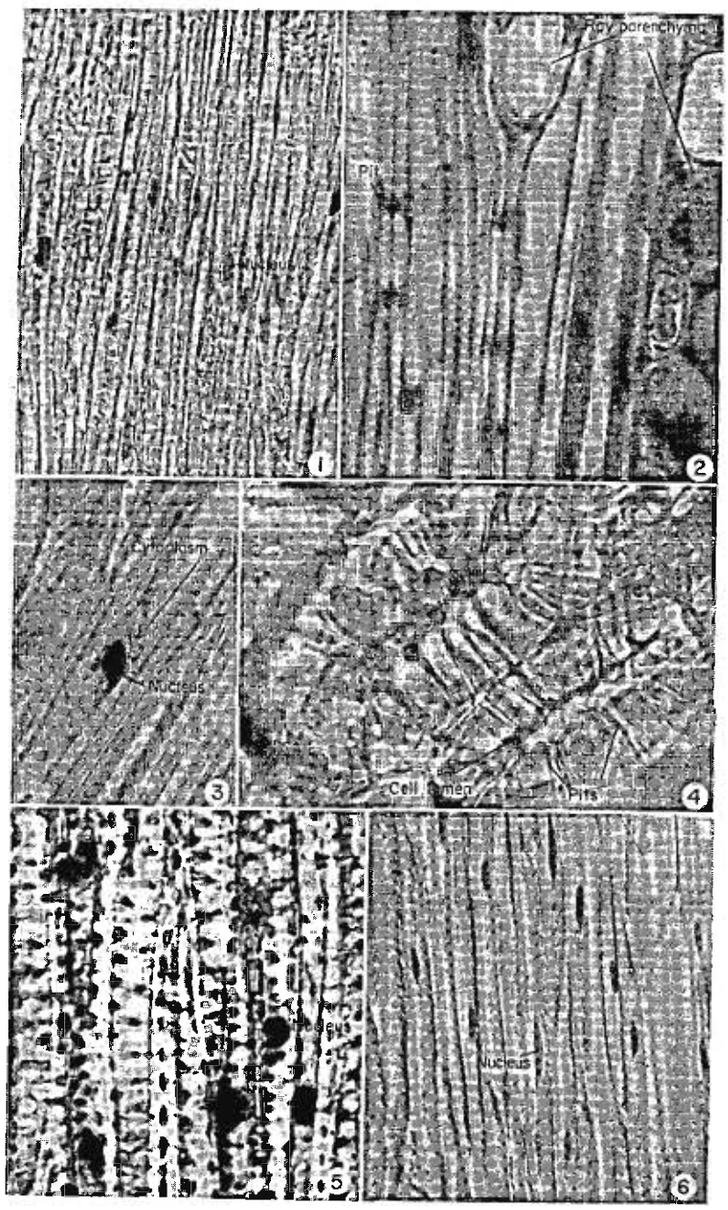


FIG. 37. 1–3, Tips of elements from the secondary xylem of *Quercus ithaburensis*. 1, Tracheid. 2, Fibre-tracheid. 3, Libriform fibre. 4, Septate fibre of *Vitis*. 5, Isolated sclereids from the leaf blade of *Olea*. (No. 5, adapted from Arzee, 1953a.)

found that this process is gradual so that new lamellae of the secondary wall are added centripetally in the form of cylinders which are open at both ends. At the same time the first-formed lamellae continue to elongate towards the fibre ends which they reach only when the fibre ceases to elongate (Fig. 36, nos. 1–8). According to Kundu and Sen (1960) the upper ends of ramie fibres continue to grow for a longer period than the basal ends. Sometimes not all the lamellae reach the actual fibre end and in some fibres chambers may be formed in the terminal portions by the ingrowth,


Ray parenchyma
Pit
1
2
Cytoplasm
Nucleus
3
Cell lumen
Pits
4
5
Nucleus
6

toward the cell lumen, of these lamellae. The lamellae of the primary phloem fibres, or at least of the immature fibres, are often not strongly attached one to another. This feature is easily demonstrated during the cross-sectioning of such material when the different layers become torn one from the other. In short fibres, such as those found in *Agave*, *Sansevieria* and *Musa textilis*, whose total length is not more than a few millimetres, all portions of the cell wall grow at the same rate.

Differences exist in the manner of growth of the fibres in the primary body and of those in the secondary body. The initials of the primary fibres appear early, before the organ in which they occur has elongated, and so they may grow in length symplastically together with the neighbouring cells which continue to divide. The symplastic growth is augmented by intrusive and gliding growth of the ends which thus penetrate between the surrounding cells. The initials of the secondary fibres develop in organs that have ceased to elongate and therefore the growth of secondary fibres can be intrusive only. This is apparently the reason why the primary fibres are usually longer than the secondary fibres of the same plant. Thus it was found in ramie that the average length of the primary phloem fibres is 164·5 mm while that of the secondary phloem fibres is 15·5 mm.

FIBRE PROTOPLASTS

During the development of primary phloem fibres of *Nicotiana* and *Linum*, Esau (1938, 1943) observed that the protoplast was multinucleate. The protoplast in developing secondary fibres usually has a single nucleus.

Mature libriform fibres and fibre-tracheids were usually regarded as being dead supporting structures. In mature fibres the presence of a living protoplast and nucleus had been described only in phloem fibres (Kallen, 1882) and in septate fibres (Spackman and Swamy, 1949). According to Bailey (1953), libriform fibres sometimes retain their living contents subsequent to the formation of the thick, lignified secondary wall, thus enabling these cells to assume a storage function in addition to that of support.

FIG. 38. 1, Micrograph of a longitudinal section of the secondary xylem of *Noëa mucronata* showing nuclei in the fibres. ×400. 2, Tangential longitudinal section of the secondary xylem of *Eucalyptus camaldulensis* in which the common wall between two fibres and pits characteristic of fibre-tracheids can be distinguished. ×950. 3, Portion of a longitudinal section of the secondary xylem of *Tamarix aphylla* in which a fibre containing cytoplasm and nucleus can be distinguished. ×680. 4, Brachysclereids as seen in a cross-section of the stem cortex of *Hoya carnosa*. ×600. 5, Portion of a longitudinal section of the secondary xylem of *Teucrium polium* showing fibre-tracheids with nuclei. ×630. 6, Portion of a longitudinal section of the secondary xylem of *Rubia velutina* showing fibres with nuclei. ×210.

Recently, however, living protoplasts and nuclei have been identified in libriform fibres of many species, and even in fibre-tracheids (Fig. 38, nos. 1, 3, 5, 6). Such living fibres were found to occur in the wood of *Tamarix* spp., in many woody species of the Chenopodiaceae, and shrubs and subshrubs of many other dicotyledonous families (Fahn and Arnon, 1963; Fahn and Leshem, 1963). Living protoplasts have also been found in many monocotyledonous fibres. In fibres with long, narrow lumina the nuclei are usually elongated (Fig. 38, nos. 1, 3, 6). The life span of the wood fibres of *Tamarix aphylla* is about 20 years.

EVOLUTION OF XYLARY FIBRES

As has been mentioned above, the xylary fibres differ in shape, size, thickness of wall, type and amount of pits. It is assumed, from the evolutionary point of view, that fibres have developed from tracheids. This assumption is supported by the fact that many transitionai forms between these two types of elements are found in some angiosperms, as, for example, *Quercus* spp. From the many transitional forms that have been distinguished it appears that the following changes have taken place during the course of the evolution of fibres from tracheids. The wall has become thickened, the number of pits and the size of the pit chamber has been reduced leading to the eventual disappearance of the bordered pit, and the cells have become shortened. This assumed shortening of the fibres refers to the shortening of the initials of the fibres in the cambium and not to the mature fibres. In the mature tissues of one plant, the libriform fibres are usually longer than the tracheids, and this increased length is secondary and is the result of the additional growth of the ends of the fibres.

STRUCTURE AND USE OF COMMERCIAL FIBRES

The term fibre, as used in industry, does not generally have the same meaning as that defined by botanists. For instance, the commercial fibres of *Linum*, *Boehmeria* and *Corchorus* are, in reality, a bundle of fibres and those from monocotyledonous leaves, such as from *Agave*, *Musa textilis*, and others, are usually the vascular bundles with the surrounding sheaths of fibres. From some plants the commercial fibres comprise the vascular system of the root, e.g. *Muhlenbergia*, or of the entire plant, e.g. *Tillandsia*. The commercial fibres of *Gossypium* (cotton) are the epidermal hairs of the seeds. Kapok fibres are hairs produced on the inner surface of the capsule of *Ceiba pentandra*.

Commercial fibres are divided into two types—hard fibres and soft fibres. Hard fibres are those which have a high lignin content in the walls,

and are of a stiff texture. Hard fibres are obtained from monocotyledons. Soft fibres may or may not contain lignin, they are flexible and elastic, and are of dicotyledonous origin. The best-known plants from which hard

FIG. 39. 1, Processed fibres of *Linum;* fibres of cylindrical shape. ×120. 2, Processed fibres of *Gossypium;* fibres are flat. ×120. (From E. Liebert, in *Handbuch der Mikroskopie in der Technik*, Umschau Verlag, 1951.)

fibres are produced are different species of *Agave*, especially *A. sisalana*, *Tillandsia usneoides*, *Musa textilis*, *Furcraea gigantea* and *Phormium tenax*. Soft fibres are mainly produced from *Linum usitatissimum* (flax) (Fig. 39, no. 1), *Cannabis sativa* (hemp), *Boehmeria nivea* (ramie), *Corcho-*

rus capsularis (jute), *Hibiscus cannabinus* (kenaf) and *Ceiba pentandra* (kapok).

The fibres of cotton, which are produced from the indumentum of seeds (Fig. 39, no. 2), represent the most important commercial fibres in use today.

Fibres are also classified according to their use (Schery, 1954): (a) textile fibres which are used in the manufacture of fabrics; (b) cordage fibres; (c) brush fibres such as are used in the manufacture of brushes and brooms; and (d) filling fibres such as those used for stuffing upholstery, mattresses and life-belts, caulking (barrels, plumbing) and reinforcing (wall plates, plastics).

In the textile industry the principal fibre used is cotton and, in smaller amounts flax, ramie and hemp. For coarser fabrics, such as sacking and bagging, jute is principally used, and cotton, flax, hemp and a few other hard fibres are used to a lesser extent. For the manufacture of twine, jute, cotton, hemp and, to a lesser extent, flax and several hard fibres are used. Ropes and binder twines are manufactured from hard fibres, such as those of *Musa textilis* (abaca) and *Agave* spp. (sisal), and to a small extent from cotton and other soft fibres. Brushes and brooms are made from *Agave* fibres, fibres from the stems and leaves of the Palmae and the inflorescences of *Sorghum vulgare*, among others. As filling fibres, the fibres of *Ceiba pentandra* (kapok), cotton, jute, the fibres of *Tillandsia usneoides*, several hard fibres and others are used. For caulking fibres, hemp, jute and sisal are used.

From a technological point of view, the shape of the fibre cell, its length and wall structure are of importance in the fibre industry. Special attention is paid to the length of the fibre, the extent to which neighbouring fibres overlap, how they are joined to one another and to the fibrillar structure of the wall.

Commercially, fibres are ranked according to durability, tensile strength, length of the strands, fineness, uniformity and elasticity. On the basis of the above features some of the most important commercial fibres may be divided into the following four ranks:

	Rank 1	Rank 2	Rank 3	Rank 4
Hard fibres	*Musa textilis*	*Agave* spp.	*Phormium tenax*	*Furcraea gigantea*
Soft fibres	*Linum usitatissimum*	*Boehmeria nivea*	*Cannabis sativa*	*Corchorus capsularis*

Sclereids

FORM AND LOCALIZATION OF SCLEREIDS

Sclereids occur in many different places in the plant body. In many plants they occur as hard masses of cells within soft parenchyma tissue. Certain organs, such as the shell of walnuts and many other stone and seed coats, are built entirely of sclereids. In many plants sclereids appear as idioblasts, i.e. as cells which are readily distinguished from the surrounding cells of the tissue by their size, shape and the thickness of their wall. Idioblastic sclereids are very variable in shape. Sclereids of peculiar shape are found in the leaves of various plants, e.g. in *Camellia*, *Trochodendron*, *Nymphaea* and *Olea* (Fig. 41), in the reduced leaves and the stem cortex of *Arthrocnemum* (Fig. 40, no. 2), and in the aerial roots of *Monstera*. In *Arthrocnemum glaucum* sclereids appear at the end of the veins, a phenomenon that was discussed for other plants by Foster (1946). Tschirch (1889) suggested the division of sclereids into four types: (1) *brachysclereids* or *stone cells* which are more or less isodiametric in form; such sclereids are usually found in the phloem, the cortex and the bark of stems and in the flesh of such fruits as pears (*Pyrus communis*) and quinces (*Cydonia oblonga*) (Fig. 38, no. 4); (2) *macrosclereids* which are rod-shaped sclereids; such sclereids often form a continuous layer in the testa of seeds, e.g. in the seeds of the Leguminosae (Fig. 40, no. 1); (3) *osteosclereids* which are bone- or spool-shaped sclereids, the ends of which are enlarged, lobed and sometimes even somewhat branched; such sclereids are mainly found in seed coats and sometimes also in the leaves of certain dicotyledons (Fig. 40, no. 1); (4) *asterosclereids* which are variously branched and often star-shaped; such sclereids are mainly found in leaves (Fig. 37, no. 5).

ONTOGENY OF SCLEREIDS

Typical brachysclereids develop from parenchyma cells by secondary thickening of the cell wall. This secondary wall is very thick and numerous concentric layers and branched pits can usually be distinguished in it. The physiological reasons for the sclerification of the parenchyma cells is not known, but Bloch (1944) thought that the fact that stone cells often appear close to wound tissues suggests that they develop in response to some physiological disturbances. In the bark the change of many parenchyma cells to sclereids suggests that, in this case, the cause is the aging of the tissue.

Another interesting example of the development of stone cells is in the continuous cylinders of the phloem fibres. When stems of plants with such cylinders grow in width, neighbouring parenchyma cells penetrate into the spaces formed between the fibres of the cylinder. The parenchyma cells then divide and become sclerified and so close the gaps formed in the cylinder (Haberlandt, 1918).

As a result of investigation of the ontogenetic development of the branched type of sclereids in the leaves of *Trochodendron aralioides* and *Mouriria huberi* (Foster, 1944, 1945, 1947), of *Memecylon* spp. (Rao, 1957), of *Olea* (Arzee, 1953a, b) and in the aerial roots of *Monstera* (Bloch, 1946),

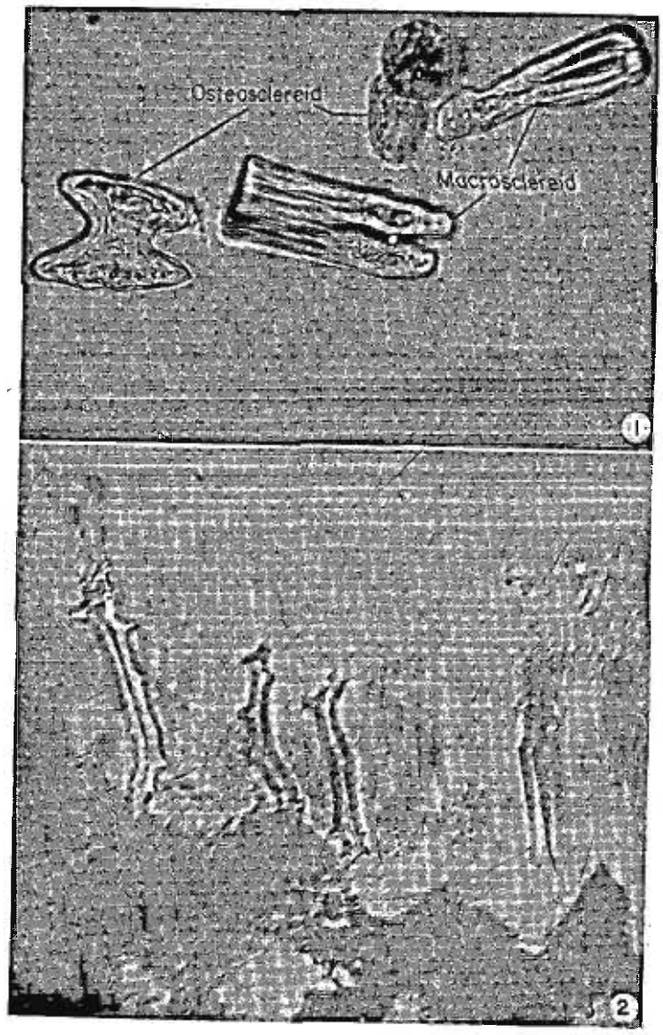


FIG. 40. 1, Isolated osteosclereids and macrosclereids from a maceration of the seed coat of *Pisum sativum*. ×500. 2, Sclereids with projections as seen in the stem of *Arthrocnemum glaucum* cleared by treatment with lactic acid. ×80.

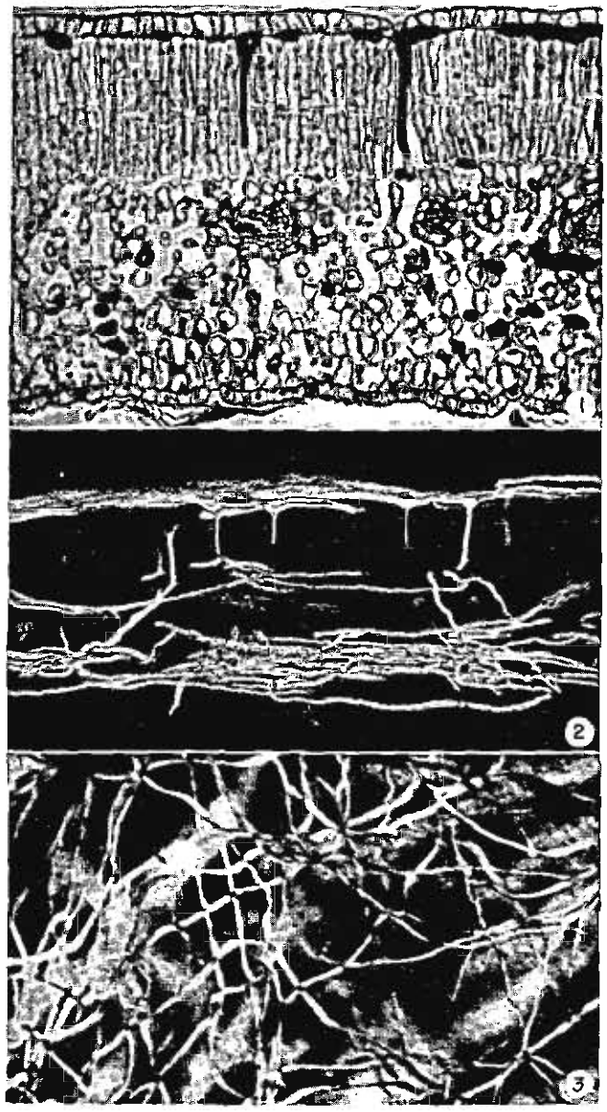


FIG. 41. Sclereids in the leaf blade of *Olea europaea*. 1, Portion of a cross-section of the blade in which parts of the sclereids (darkly stained) can be seen. ×160. 2, Portion of a relatively thick, cleared cross-section of the leaf blade photographed in polarized light in which the sclereids appear white. ×95. 3, Surface view of portion of a cleared leaf, photographed in polarized light, showing the arrangement of the sclereids in the spongy parenchyma. ×110. (From Arzee, 1953a.)

the following histogenetic facts have been realized. In all the above examples the sclereids develop from small initials with thin walls which, already in the early stages of development, begin to branch and so acquire the form of the mature sclereid. The branches or projections of the sclereid penetrate into the intercellular spaces, but intrusive growth of these branches, between the joined walls of neighbouring cells, is also common (Fig. 42, nos. 1–3). The degree of pitting in these sclereids is not constant.

Sclereids are usually described as non-living cells when mature, but it has been seen that the protoplasts may remain viable throughout the life of the organ in which the sclereids are found. In non-deciduous leaves and in certain stems the life of the sclereids may sometimes be 4–5 years (Puchinger, 1923). The protoplast in the stone cells in the fruits of the pear and quince also remains alive for relatively long periods. According to Alexandrov and Djaparidze (1927), during the ripening of the quince fruit, the stone cells undergo a process of delignification, which they believe is an indication of the enzymatic activity of the protoplast of the stone cell itself.

The structure of the fibre wall has been investigated comparatively thoroughly and emphasis has been laid on the wall structure of fibres that are of economic value. Attention has also been paid to the ontogenetic and phylogenetic development of fibres. Cell growth, especially intrusive growth, can be well studied in the course of fibre development.

As was mentioned in the chapter dealing with collenchyma, collenchyma cells may often become sclerified during the maturation of the organs in which they occur. This fact emphasizes the view of the close relationship between these two tissues.

Because of the great variability in the form of fibres and because of the existence of many transitional forms, fibres serve as favourable material for the study of the evolution of an element or part of it, as, for instance, the evolution of the pit.

Substitute and septate fibres have, during the course of evolution, become strikingly different from the typical fibre form and should, actually, be classified as parenchyma cells with secondarily thickened walls. A substitute fibre resembles an elongated parenchyma cell and a septate fibre a longitudinal series of parenchyma cells derived from a single mother cell

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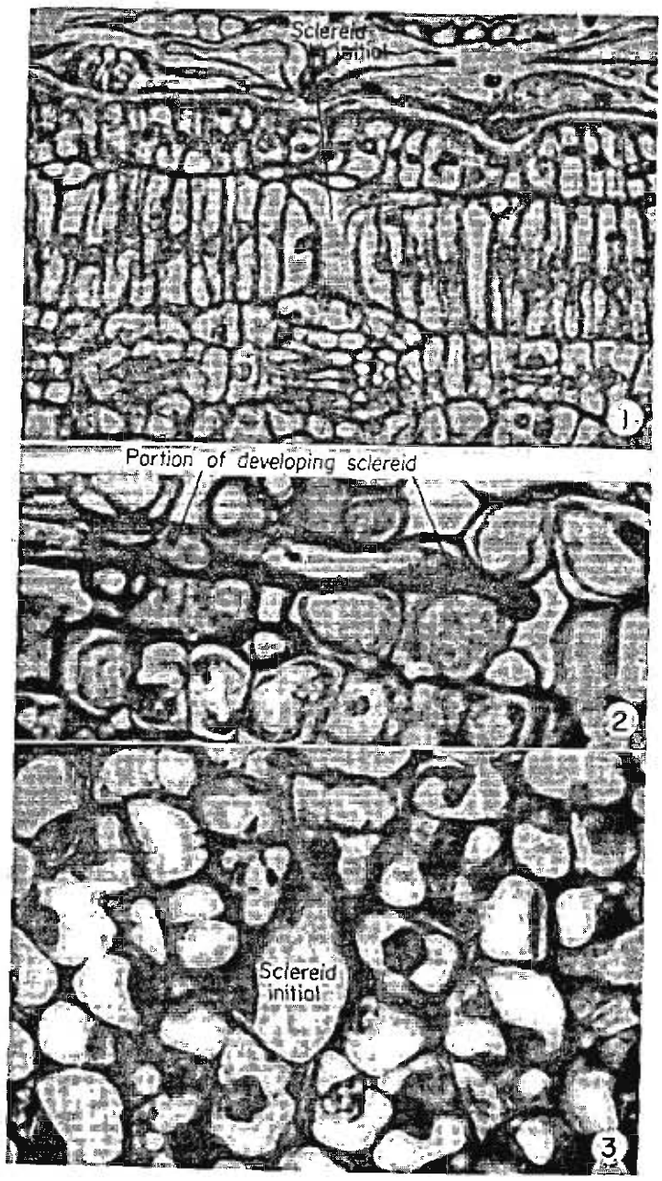
FIG. 42. Stages of development of sclereids in the leaf blade of *Olea europaea*. 1, Portion of a cross-section of a young leaf in which a sclereid initial can be distinguished in the as yet single row of palisade cells. ×370. 2, Portion of cross-section of a leaf blade, showing the intrusive growth of an arm of a developing sclereid. ×940. 3, Portion of a section cut parallel to the blade surface in which a sclereid initial can be seen. ×210. (From Arzee, 1953b.)


Sclereid initial
1
Portion of developing sclereid
2
Sclereid initial
3

in which secondary wall lamellae develop before the cell divisions are completed.

The libriform fibres and the fibre-tracheids have, till recently, generally been described as non-living cells devoid of protoplasts and were regarded as having only mechanical function or, at the most, as playing a small role in water conduction in addition to the tracheary elements. However, it now appears, in the light of recent research, that the libriform fibres and even fibre-tracheids of the sap wood of many woody plants contain living protoplasts. Therefore we should begin to consider fibres not only as supporting elements but also as elements that doubtless fulfill various other important physiological functions. This aspect, the investigation of which has been initiated in our laboratory, awaits still further research.

It is possible that the retention of living protoplasts in fibres is more characteristic for certain life forms (e.g. shrubs and subshrubs) or for woody plants of certain habitats, such as xeric ones. The evolutionary and ecological investigation of these assumptions may possibly bring to light some interesting results.

It is also worth mentioning that the appearance of the living protoplasts in libriform fibres and fibre-tracheids represents a further example of the indistinct limits between the various elements that form the highly differentiated tissues of the higher plant body. This, together with similar phenomena, are of great importance in our understanding of the evolution of the various elements.

The appearance of idioblastic sclereids in the leaves of plants that belong to diversified taxonomic and ecological groups makes it difficult to understand both their evolutionary and functional significance.

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CHAPTER 7

XYLEM

THE vascular system of the sporophytes of the higher plants consists of *xylem*, the main function of which is the transport of water and solutes, and *phloem* which mainly transports the products of photosynthesis.

On the basis of its physiological and phylogenetic importance, the vascular system, and especially the xylem, has been used for the classification of a large group of plants. The term *vascular plants* was first used in 1917 by Jeffrey. Recently the term *Tracheophyta* has been introduced to cover this group of plants which comprises the Pteridophyta and Spermatophyta. The term Tracheophyta has been derived from the xylem, and not the phloem, because of the firm and enduring structure of the tracheary elements. These elements have thick, hard walls and so can be distinguished more easily than the phloem elements. Also the xylem is more readily preserved in fossils and so can be identified more easily.

Xylem is a complex tissue as it consists of several types of cells. The most important cells are the *tracheary elements* which are the non-living cells that are principally concerned with the transport of water and which also, to a certain degree, have a supporting function. Fibres are present in the xylem where they are mainly concerned with the strengthening of the plant body. Sclereids also may be sometimes present. Parenchyma cells which have storage and other functions also occur in the xylem. The xylem of some plants contains laticifers (see Chapter 9).

The xylem and phloem elongates in developing organs by the continual differentiation of new elements produced by the procambium, which itself is continuously produced by the apical promeristem. The xylem produced by the procambium in the primary body is called the *primary xylem*. In many plants, after the completion of the formation of the primary body, secondary tissues are developed. The xylem that is produced as a result of the activity of the vascular cambium is called the *secondary xylem*.

In the primary xylem the elements that are completed early, i.e. the *protoxylem*, are distinguished from those completed later, i.e. the *metaxylem*.

Tracheary elements

Two basic types of tracheary elements are distinguished—*tracheids* and *vessel members*. The term tracheid was introduced in 1863 by Sanio who discussed the similarity and differences between this element and the vessel member. Since then much work has been devoted to the investigation of the structure, shape, function, ontogeny and phylogeny of these elements.

The main difference between tracheids and vessel members is that the former are not perforated while the end walls of the latter are perforated (Fig. 45). A vessel, which is also termed a *trachea*, is built of numerous vessel members that are joined one to the other by their end walls. Vessels are terminated by a vessel member of which the proximal end wall is perforated, whereas the distal end wall is not, i.e. the distal parts of a vessel is tracheid-like.

STRUCTURE AND SHAPE OF THE SECONDARY WALL OF TRACHEARY ELEMENTS

In a radial longitudinal section of vascular bundles it can be seen that the tracheary elements differ one from the other in the shape and structure of the secondary wall. In many plants the secondary wall thickening of the first-formed xylem (protoxylem) is annular or helical (Fig. 43, nos. 7–9; Fig. 44, no. 1). The helical thickening may be single, or more than one helix may be present in a single element. The rings or helices may be arranged in a loose or a dense manner. From an ontogenetic viewpoint, the annular elements precede the helical elements. In later-formed tracheary elements the helical bands become joined in certain areas giving rise to a ladder-like type thickening; such thickening is termed *scalariform thickening* (Fig. 43, no. 10). In tracheary elements formed at a still later ontogenetic stage the wall thickening is in the form of a network, i.e. *reticulate thickening* (Fig. 43, no. 11). When the openings in the secondary wall of such a network are elongated in a direction perpendicular to the longitudinal axis of the element, the thickening is termed *scalariform-reticulate*. In the ontogenetically most advanced elements, the secondary cell wall is interrupted only at the pits; such elements are termed *pitted elements* (Fig. 44, no. 2). Pitted elements are characteristic of the late primary and of the secondary xylem. Not all the above types are always found in a single plant. On the other hand, intermediate types not mentioned above can be found, as well as combinations of more than one form of thickening which may occur in a single element. The annular and helical wall thickenings may vary in thickness and certain helices are so deeply grooved on their inner surfaces as to appear double (Fig. 43, no. 6). In some cases the helical thickening is joined by a narrow strip to the primary wall (Fig. 43, [illegible])

The pits in pitted tracheary elements are bordered. The well-developed bordered pit-pairs which are usually present between two tracheary elements are termed *intervascular pits*. Between tracheary elements and fibres there may be only a few small pits or even none at all. Between tracheary

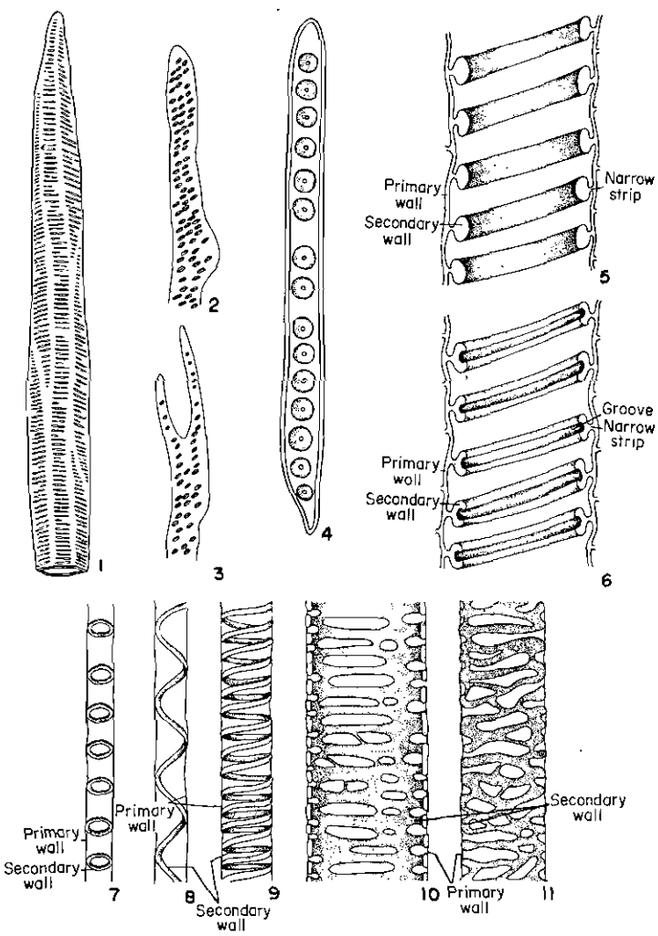

FIG. 43. 1, Tip of tracheid of *Dryopteris;* with scalariform pitting. 2 and 3, Tips of tracheids of *Kingia*. 4, Tracheid of *Pinus*. 5, Portion of a longitudinally sectioned tracheary element showing the helical wall thickenings and the strips by which they are joined to the primary wall. 6, As in no. 5, but in which the helical thickening is deeply grooved. 7–11, Different types of wall thickening in tracheary elements. 7, Annular thickening. 8, Helical thickening. 9, Dense helical thickening. 10, Scalariform thickening. 11, Reticulate thickening.

elements and parenchyma cells the pit-pairs are mostly half-bordered, i.e. bordered on the side of the tracheary element and simple on the side of the parenchyma cell.

When the bordered pits are transversely elongated and are arranged in longitudinal rows along the element, the pitting is termed *scalariform pitting* (Fig. 18, no. 2). Circular and elliptical pits are arranged in horizontal or diagonal rows. The former arrangement is called *opposite pitting* (Fig. 18, no. 4) and the latter *alternate pitting* (Fig. 18, no. 5). On the inside surface of a pitted secondary wall a helical thickening may develop (Fig. 132).

In the Ophioglossales, the Ginkgoales, the Coniferales and the Gnetales no scalariform pitted elements are found. In plants of these orders bordered pits, which are similar to those found in the secondary tracheary elements of the same plant, are found on the reticulate and helical thickenings of the primary xylem (Fig. 46, no. 10).

The following facts are known about the formation of the special wall thickenings of the tracheary elements.

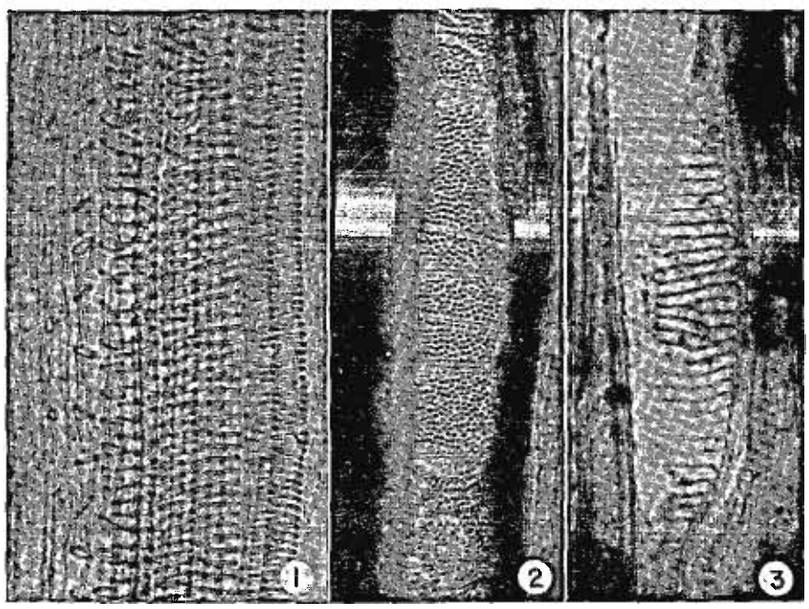

FIG. 44. 1 and 2, Micrographs of longitudinal sections of the young stem of *Cucurbita*. ×150. 1, Protoxylem elements with annular and helical thickening. 2, Pitted metaxylem vessel. 3, Micrograph of a radial longitudinal section in the secondary xylem of *Viburnum tinus* showing a scalariform perforation plate. ×470.

Crüger (1855) observed that in the positions where the thickenings of the secondary wall will develop, strips of actively streaming cytoplasm appear. Similar conclusions were reached by Barkley (1927) who believed that the position of the cytoplasmic strips is determined by the position of rows of vacuoles.

A similar phenomenon was also observed by Sinnott and Bloch (1945) who studied the development of tracheary elements from parenchyma cells during the regeneration in the vascular bundles of *Coleus*. Interesting observations were made by Majumdar (1940, 1941) who worked on the development of vessels in the protoxylem of *Heracleum*. Recently Wooding and Northcote (1964) suggested that the Golgi apparatuses are involved in the formation of the wall thickenings.

There is also evidence that the cytoplasm of the developing tracheary element lines the cell wall with suberin (Scott *et al.*, 1960).

The functional significance of the different types of wall thickenings in the tracheary elements is not clear. It is possible that the exclusive appearance of annular and spiral thickenings in elements in those organs that are still elongating has some connection with the rapid increase in length of the organ. Investigations using X-rays together with the regulation of light which altered the rate of stem elongation proved this assumption. Goodwin (1942) and Smith and Kersten (1942) saw that if stem elongation is inhibited the production of annular and spiral vessels is reduced or stopped and pitted vessels develop.

VESSELS AND THE STRUCTURE OF PERFORATION PLATES

As has been mentioned previously, two main types of tracheary elements can be distinguished—tracheids and vessel members. Tracheids are non-perforated cells in which only bordered pit-pairs are found in the areas of contact between them, while vessel members are perforated at their ends. By these perforations the vessel members become joined to form a tube-like series of cells which is termed a *vessel* or *trachea*. Vessels are limited in length and those vessel members which terminate a vessel are perforated on one end only, i.e. the terminating end is not perforated. Therefore the passage of water from vessel to vessel takes place via the pits as from tracheid to tracheid. It is difficult to measure the length of vessels but this was done successfully by Handley in 1936 who made use of the fact that, although water and solution pass through the pits, gas does not. Handley forced coal gas into one end of a cut branch and attempted to light it at the other end. From such experiments he came to the conclusion that the length of the vessels in *Acer* is about 60 cm and in *Fraxinus* about 3 m.

The vessel members are usually perforated on the end walls but some-

times the perforations are formed on the side walls. Those parts of the cell wall that bear perforations are called *perforation plates*. The perforation plate may contain one large perforation and then it is termed a *simple perforation plate* (Fig. 45, nos. 4–6), or it may contain numerous perforations. In the latter case there are several possible ways in which

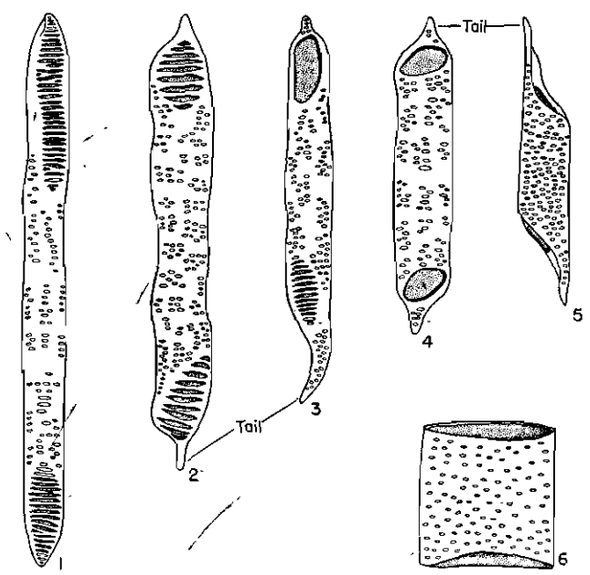

FIG. 45. Dicotyledonous vessel members. 1 and 2, Vessel members in which the perforation plates at both ends are scalariform. 3, Vessel member with one scalariform and one simple perforation plate. 4–6, Vessel members with simple perforation plates. "Tails", the narrow elongated tips of the vessel members, can be seen in nos. 2–5. (Adapted from Bailey.)

the perforations can be arranged. When the perforations are elongated and are arranged in a parallel series the plate is termed a *scalariform perforation plate* (Fig. 44, no. 3; Fig. 45, nos. 1, 2), when in a reticulate manner, *reticulate perforation plate* (Fig. 46, nos. 2, 4) and when the perforations are almost circular the plate is termed a *foraminate perforation plate* (Fig. 46, no. 11).

The scalariform perforation plates may sometimes be very long and then they contain hundreds of perforations. In such cases the end wall bearing the plate is very long and oblique so that it is sometimes difficult to decide whether it is a vessel member or a tracheid. The identity of these elements can be established by passing a carbon suspension through sectioned portions of branches. The suspended particles can pass only

through perforations as the pit membrane prevents their passage through the pits. However, sometimes even the above method is not reliable and a further method in which very fine longitudinal sections of the perforation plate are cut, is used in order to discover if the primary wall is present or

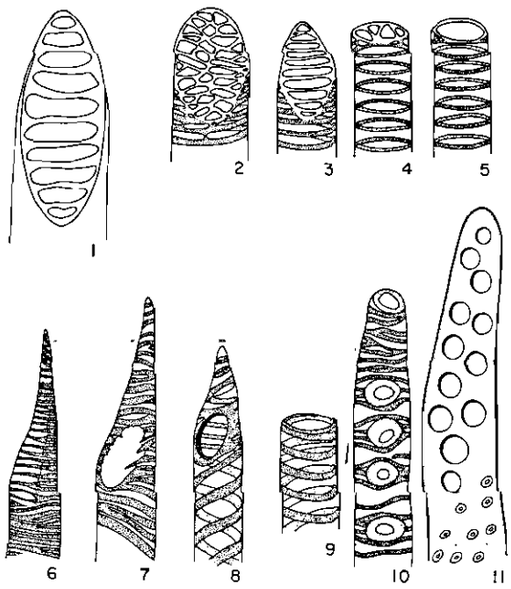

FIG. 46. 1–5, Perforation plates of vessel members in the primary xylem of monocotyledons. 1, Scalariform perforation plate from the stem of *Phoenix dactylifera*. ×70. 2, Reticulate perforation plate from the root of *Hymenocallis caribaea*. ×200. 3–5, Vessel members from the stem of *Rhoeo discolor*. ×150. 3, Scalariform perforation plate of a helically-thickened vessel member. 4, Reticulate perforation plate of an annularly-thickened vessel member. 5, Simple perforation plate. 6–9, Ends of vessel members with helical thickening from dicotyledonous primary xylem. 6, Scalariform perforation plate. 7, Transitional form between a scalariform and simple perforation plate. 8 and 9, Simple perforation plates. 10, Tracheid of *Gnetum* with helical thickening and circular bordered pits. 11, Vessel member end of *Ephedra* with a foraminate perforation plate. (Nos. 1–5, adapted from Cheadle, 1953; nos. 6–10, adapted from Bailey, 1944.)

not. This method also involves technical difficulties. It may be that som of the gaps in the secondary wall are perforations and some are pits It has been suggested that such intermediate forms between typica tracheids and typical vessels should be termed *vessel-tracheids* (Fahn 1953) or *vessel-member-tracheids* by analogy with fibre-tracheids, whicl are intermediate between fibres and tracheids.

In many dicotyledonous species the middle portion of the vessel members of the secondary xylem widens during ontogenetic development while the tips remain narrow and elongated. These tips are not perforated and they appear as projections that overlap the walls of the neighbouring vessel members; these tips have been termed *tails* (Chalk and Chattaway, 1934, 1935). The perforations are present at the end of the widened part of the element, i.e. near the base of the tails (Fig. 45, nos. 2–5).

DEVELOPMENT OF VESSELS

Vessels develop from meristematic cells — procambial cells in the primary xylem and cambial cells in the secondary xylem. The vessel members may or may not elongate prior to the thickening of the wall but they usually widen in this stage of development.

Much attention has been paid by workers studying the ontogeny of vessels to the end walls in which the perforations develop. Different opinions exist as to how the perforations develop. According to Esau and Hewitt (1940), who worked on herbaceous plants in which the vessel members had simple perforation plates, layers of the secondary wall are deposited on the primary wall in the pattern specific for each type of vessel after the vessel members have reached their maximum size. Those parts of the primary wall in the position where the perforation will develop do not become covered with secondary wall substance, but they become thicker relative to the other area of the primary wall of the element (Fig. 47, nos. 1–3). This thickening apparently is not the result of the addition of material to the wall but the result of the swelling of intercellular substance. After the secondary walls are completely developed and lignified the swollen parts of the primary wall and middle lamella slowly disintegrate. This process is apparently brought about by the protoplast which itself later dies and disintegrates (Fig. 47, no. 4).

According to Priestley *et al.* (1935), who investigated the development of the vessels in trees, the production of the perforation in the end wall is a sudden process and no intermediate stages can be found. Apparently, while the walls are still very thin, the end walls contract suddenly, and so the rim or rims around the perforations are formed (Fig. 47, no. 5). Often a stretched pectic membrane remains in the position of the perforation. By means of plasmolysis the above workers were able to show that each vessel member has a separate protoplast during all stages of the thickening and lignification of the wall.

In ring-porous and sometimes in diffuse-porous wood, in which the vessels are wide, as the vessel grows in width the cells neighbouring it may become separated one from the other. In this way the vessel is brought into contact with new cells (Fig. 47, nos. 6, 7). In many cases it is possible to

observe that where the position of the above separating cells is shifted relative to the widening vessel, the cells retain their original attachments, or at least partially so, in those positions where there are pits. This is possible by the extension of the cell wall to form bridge-like connections in the region of the pits (Fig. 47, no. 8). According to Priestley *et al.* (1935) this

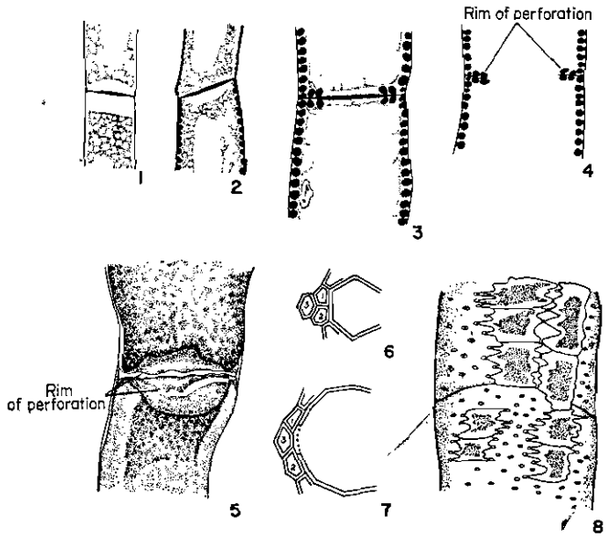

FIG. 47. 1–4, Development of a perforation plate in vessel members of *Apium graveolens*, after Esau, 1936. The development of helical secondary thickening on the side walls and the presence of the primary end wall can be seen in nos. 1–3. The end wall has disappeared in no. 4. 5, End portions of two adjacent vessel members of *Fraxinus* in which it is possible to distinguish the perforation rim and the two protoplasts that have separated from one another. ×125. 6 and 7, Diagrams of cross-sections of a vessel and neighbouring cells showing how the vessel, during enlargement, comes into contact with new cells. Neighbouring cells indicated by numerals. 8, Drawing of portion of a vessel of *Ulmus* in surface view, showing how the cells around the vessel tear away from each other as a result of the widening of the vessel. The neighbouring cells retain their original attachments to the vessels where there are pits, resulting in the formation of bridge-like extensions. ×95. (Nos. 5–8, adapted from Priestley *et al.*, 1935.)

phenomenon is apparently made possible because of the greater plasticity of the pits themselves or their margins. These workers state that in ring-porous wood the cells surrounding the vessels differentiate prior to the vessels or, at latest, simultaneously with them and therefore the above separation takes place. In diffuse-porous wood the walls of the cells next to the vessel become thickened and lignified somewhat later than those of the vessel members.

PHYLOGENETIC DEVELOPMENT OF TRACHEARY ELEMENTS

The xylem holds an important position in the study of plant tissues as the structure of its elements is of extreme importance in taxonomy and phylogeny. More attention has been paid to the phylogenetic development of xylem than to any other tissue. The structure of the tracheary elements has been studied in special detail. The research has been aided by statistical methods which emphasize the differences in structure and shape of the tracheary elements and which have explained their phylogenetic significance.

It has been obvious for a long time that the tracheid is a more primitive element than the vessel member. The tracheid is the only tracheary element found among Pteridospermae, in fossil Spermatophyta, in most of the lowest vascular plants of today, and in nearly all the Gymnospermae. It is commonly accepted that vessel members have developed from tracheids. Vessel members occur in the following diverse groups of plants: in the most advanced gymnosperms, the Gnetales; in dicotyledons except for the lowermost taxonomic groups; in monocotyledons; in the fern, *Pteridium;* in certain species of *Selaginella;* and in *Equisetum* (Bierhorst, 1958). From the above it can be assumed that vessels developed independently, by parallel evolution, in each of these groups.

ORIGIN AND PHYLOGENETIC DEVELOPMENT OF VESSEL MEMBERS IN ANGIOSPERMS

In order to understand the problems of plant phylogeny, fundamental methods of logic have been used. Frost (1930 a, b; 1931) clearly defined some of these fundamental logical assumptions while trying to establish the origin of the vessels in the dicotyledons. The following are the principal assumptions used by Frost.

1. *The association method.* This method states that if it is possible to determine which of two structures is the more primitive, and if it is assumed that the two structures have a direct genetical relationship, it will be possible to conclude that the primitive condition of the more advanced structure will be similar to the general condition of the primitive structure. If there is not much similarity then the assumption of direct genetical relationship is not correct or the elements in question are, apparently, so far separated in the scale of evolution that the primitive form of the advanced element has been lost. Therefore, with reference to tracheary elements, if it is assumed that the tracheids are more primitive than the vessel members and that the two elements have a direct genetical relationship, then it must be concluded that the most primitive vessel members will be those that are most similar to tracheids.

2. *The correlation method.* By this method it is assumed that in a certain homogeneous tissue, as, for instance, the secondary xylem, there will

exist a statistically significant correlation between the degrees of specialization of the main characteristics of a structure in a large random sample (many species), i.e. the various features have undergone evolutionary changes simultaneously. Therefore, features occurring together with those features that are defined as being primitive, by the association method, are themselves primitive, and those that occur together with features defined as being advanced, are advanced. It is necessary to bear in mind that such correlations express only the general trends of development and that exceptions exist. The development of some features may be delayed and of others advanced. The investigation of these exceptions can indicate the lines of secondary specialization which only become clear after the principal lines of development have been determined. In relation to the vessel members, if great length is a primitive feature (as is derived by the association method) then all other features that are found in correlation with great length are also primitive features.

3. *The sequence method.* This method deals with the reconstruction of the evolutionary variability on the basis of the variation, as seen in living forms. These variations can be seen ontogenetically or by the comparison of different plants belonging to a single taxonomical group. The contribution of this method to the problem of the origin of vessels has been the determination of the origin of vessel members from tracheids with scalariform pitting. Typical tracheids of this type appear only in the secondary wood of those dicotyledonous genera that have no vessels, e.g. genera of the Winteraceae, Monimiaceae, Chloranthaceae and Tetracentraceae, but are completely absent from the secondary xylem of angiosperms that contain vessels (Bailey, 1944). In some trees and large shrubs of various primitive dicotyledonous families, the vessel members of the secondary xylem are similar in size, angular cross-section, pitting and thin secondary walls to tracheids with scalariform pitting. It is important to mention that the scalariform pitted tracheids have served as the origin not only of vessel members but also of tracheids with circular bordered pits and apparently also, indirectly, of fibre-tracheids and libriform fibres (Tippo, 1946; Bailey, 1936, 1953). The complete or almost complete absence of primitive tracheids with scalariform pitting in the Angiospermae is related to their development, in the process of phylogeny, into vessel members or into tracheids with a more advanced form of pitting.

The following structural features of the angiosperm tracheary elements are those that are used as a basis for the study of their evolution.

1. *The length of the element.* The tracheids are long cells whose average length reaches 4·35 mm in *Trochodendron*, a vessel-less dicotyledon (Bailey, 1944). Their average length as calculated from many hundreds of measurements made in monocotyledons is 5·07 mm (Cheadle, 1943a). In monocotyledons, according to Cheadle, vessels can be divided into four groups, according to their degree of specialization. The average lengths of the

vessel members in these four groups are 3·96 mm, 2·58 mm, 1·47 mm and 0·76 mm. As the vessel members are shorter than the tracheids the shorter the vessel member, the more advanced it is considered to be.

2. *The diameter of the element.* The diameter of the tracheid is smaller than that of the vessel member.

3. *The thickness of the wall.* The wall of a typical tracheid is thin and is of equal thickness over the entire circumference. This feature is also seen in primitive vessel members.

4. *The perforation plates.* Those scalariform perforation plates that are long, oblique and with numerous perforations are considered the most primitive and the simple, horizontal perforation plates the most advanced.

5. *The shape of the element in cross-section.* The shape of the tracheids and the primitive vessels in cross-section is angular, while that of advanced vessel members is circular or nearly so.

6. *The type of pitting.* In the dicotyledons scalariform pitting in vessel members is considered to be primitive. The structure and arrangement of pits developed, from scalariform pitting, through intermediate forms in which scalariform pits occur together with circular or elliptical pits (Fig. 18, no. 3), to forms with only circular or elliptical pits. Of this advanced type of pitting, that in which the pits are arranged in parallel rows, i.e. opposite pitting, is more primitive than alternate pitting, in which the circular or elliptical pits are arranged along more or less helical lines (Fig. 18, nos. 4, 5). The appearance of the spiral thickenings on the inside of the secondary wall of the tracheary elements is evidence of advanced development.

The phylogenetic development of the side walls of the tracheary elements was prior to that of the perforation of the end-walls.

SUMMARY OF SUGGESTED ORIGIN AND SPECIALIZATION OF VESSELS

From investigations based on the methods and facts that have been mentioned above and which have been made over the last 30 years, the present knowledge of the evolutionary development of the mono- and dicotyledonous vessel members can be summarized, after Cheadle (1953), as follows:

Dicotyledons

1. Ten woody genera are known that completely lack vessels. These genera belong to the following five families: Chloranthaceae, Winteraceae, Tetracentraceae, Trochodendraceae and Monimiaceae.

2. There are 52 out of 147 families that consist of woody plants only and that contain one or more species that have only scalariform-perforated

vessel members. The following are some of these families: Aquifoliaceae, Betulaceae, Buxaceae, Celastraceae, Magnoliaceae, Myrtaceae, Styracaceae.

3. Of 82 families that contain both woody and herbaceous species, only 7 families contain one or more species with exclusively scalariform-perforated vessel members.

4. Of the herbaceous plants, the internal structure of which has been adequately studied, only *Paeonia* of the Ranunculaceae, *Pentaphragma* of the Campanulaceae, and a few other species of three other families have exclusively scalariform-perforated vessel members. However, in these examples the perforation plate is mostly not of the very primitive type as the plate is short and has only a few perforations.

5. Of the remaining herbaceous families, in 61 families only vessel members with simple perforation plates are found and in 20 families the perforation is mainly simple but a few scalariform perforation plates (usually short) can be found.

From all the above facts it appears that in the dicotyledons the vessels arose first in woody plants. Apparently they developed independently a number of times as vessel-less species are found in different families. Because of the advanced character of the vessels in herbaceous plants it cannot be suggested that the woody plants have been derived from the herbaceous plants.

As a result of the data that have accumulated, it has been concluded that the vessels arose first in the secondary xylem and later in the metaxylem. The specialization has also gradually advanced from the secondary to primary xylem.

It can also be assumed that the herbaceous plants have developed from the woody plants by reduction of cambial activity only after obvious development of the vessel members had taken place in the woody ancestral plants.

In some specialized dicotyledons, such as certain of the Cactaceae, the secondary xylem lacks vessels which are replaced by so-called vascular tracheids. However, in such plants the lack of vessel elements is a result of secondary reduction (Bailey, 1957).

Monocotyledons

1. From a phylogenetic point of view, vessels in the monocotyledons first appeared in the roots and later in the stems and leaves. The specialization of the vessels followed the same pattern (Cheadle, 1943a, b).

2. Phylogenetically, the vessels first appeared and became specialized in the late-formed metaxylem and progressed gradually into the early-formed metaxylem and finally into the protoxylem (Cheadle, 1944).

3. Monocotyledons exist today that have, in the last-formed metaxylem of their roots, only the most primitive vessels the perforation plates of which are scalariform and which contain more than 100 parallel perforations.

4. A few monocotyledonous families with only aquatic species are known to include plants that lack vessels completely in all their organs. This feature, however, may be a secondary one.

The tracheary elements have developed during the evolution of the land plants. As has been pointed out by Bailey (1953), two main functional trends have become evident during the course of the morphological evolution of these elements, i.e. the development of those structures that enhance rapid conduction, on the one hand, and of those that strengthen the elements, on the other hand. These two trends are antagonistic to a great extent because certain structures that increase the efficiency of conduction tend to weaken the cells and vice versa. However, during the course of evolution, structures have been developed that have, to various extents, resolved these two trends.

Pitted tracheary elements, in addition to those with annular and helical wall thickenings, are found in most of the Tracheophyta, with the exception of certain lower Devonian plants and some hydrophytes. Elements with such wall thickenings give support to the mature stem. The absence of living protoplasts in the tracheary elements, the development of elongated tracheids and the occurrence of vessel members are all features that increase the efficiency of water conduction. The bordered pit-pairs which are characteristic of the tracheary elements, are, as has been shown by Bailey, well adapted to their function and they combine the two above-mentioned trends. On the one hand, the area of the pit membrane is comparatively large and so the passage of water is fairly easy and, on the other hand, the extent of the development of the secondary wall is maximal because the secondary wall overarches the pit membrane in such a manner that the pit membrane remains comparatively large whereas the pit aperture is very small. This feature greatly strengthens the tracheary elements.

In tracheids more rapid conduction is obtained by the elongation of the cells, the increase in diameter of the lumen and in the number of pits and the reduction of wall thickness. Strengthening of the tissue is brought about by the shortering of the cells, narrowing of the lumen, increase in wall thickness and the reduction in the number of pits. In the secondary xylem of conifers, for instance, the early wood is more adapted for efficient water conduction and the tracheids of the late wood, for support.

Conduction is further facilitated by the complete disappearance of the pit membranes in certain areas so resulting in the formation of vessel members. In the secondary xylem of certain primitive dicotyledons primi-

tive vessel members, resembling scalariform pitted tracheids, and thick-walled, narrow tracheids with a few round bordered pits have been observed to occur side by side. This phenomenon proves that the evolution of tracheids, in relation to function, was dichotomous, i.e. the scalariform tracheids evolved into vessel members which were better adapted to conduction, whereas the tracheids with round bordered pits are modified to give better support and, through various intermediate forms, give rise to the libriform fibres. Fibre-tracheids, which are an intermediate form, and libriform fibres functionally differ greatly from the tracheary elements and in many plants they contain even living protoplasts and store reserve materials.

From the large amount of data that has been accumulated from the study of the various angiosperm groups, it is possible to build a clear picture of the trend of evolution as has taken place in the development of the tracheary elements. The fact that this trend is unidirectional, irreversible and cannot be interpreted in the reverse direction is important and should be emphasized. The structural evolution of the tracheary elements presents one of the most convincing examples of evolutionary development. However, although it is obvious from the great amount of data, that this structural evolution has been accompanied by functional specialization, as yet almost nothing is known about whether or not a correlation exists between the types of tracheary elements and ecological conditions. This is a problem that still needs to be investigated.

The sequence of the different types of tracheary elements and the numerous transitional forms are important features in the study of the origin of the Angiospermae and the phylogeny of the various taxonomic groups among them. It is still necessary, however, because of parallel and convergent evolution, to accumulate more data concerning the tracheary elements of the various species and to use such data together with morphological and structural data concerning other elements and tissues, before any definite conclusions can be drawn (Fahn, 1954).

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CHAPTER 8

PHLOEM

THE phloem together with the xylem constitute the conducting system of vascular plants. The xylem functions principally in the conduction of water, and the phloem of products of photosynthesis. Similarly to the xylem the phloem also is a compound tissue. The important cells of the phloem are the *sieve elements* which serve for the conduction of the photosynthetic products. Additional to these elements phloem contains typical parenchyma cells in which reserve substances are stored, as well as specialized parenchyma cells, i.e. the *companion cells* and *albuminous cells*, which are connected with the functioning of the sieve elements. Fibres, sclereids and sometimes laticifers may also be found in phloem tissue.

The primary phloem, similarly to the primary xylem, develops from the procambium. The primary phloem is divided into the *protophloem*, which develops from the procambium during an early ontogenetic stage, and the *metaphloem* which also develops from the procambium, but at a later stage of development.

The sieve elements were first discovered by Hartig in 1837 and the term phloem was coined, from the Greek word for bark, by Nägeli in 1858.

The phloem in the stem, is usually external to the xylem but in some ferns and in different species of numerous dicotyledonous families, e.g. Asclepiadaceae, Cucurbitaceae, Myrtaceae, Apocynaceae, Convolvulaceae, Compositae and Solanaceae, phloem is also present on the inside of the xylem. Phloem on the inside of the xylem is called *internal* or *intraxylary phloem* (Fig. 70, no. 3) and it develops a little later than the external phloem. In certain families, such as the Chenopodiaceae, Amaranthaceae, Nyctaginaceae, Salvadoraceae and others, phloem is also present within the secondary xylem. This type of phloem is called *interxylary phloem* or *included phloem* (Fig. 158, nos. 1–3).

Sieve elements

The most characteristic features of sieve elements are the *sieve areas* in the walls and the disappearance of the nucleus from the protoplast.

The sieve areas are interpreted as being modified primary pit fields and they appear as depressions in the wall in which groups of pores are lo-

cated. *Connecting strands*, which are structures resembling plasmodesmata but which are thicker, pass through these pores and so connect the protoplasts of the neighbouring sieve elements (Fig. 50, no. 1; Fig. 51, no. 1). Sieve areas can be distinguished from primary pit fields by the following two features: (a) in the sieve areas the connecting strands are much thicker than the plasmodesmata that occur in the primary pit fields; (b) in the sieve area each pore contains a small cylinder of *callose* which surrounds the connecting strand (Fig. 48, nos. 2–4; Fig. 51, no. 1). The diameter of

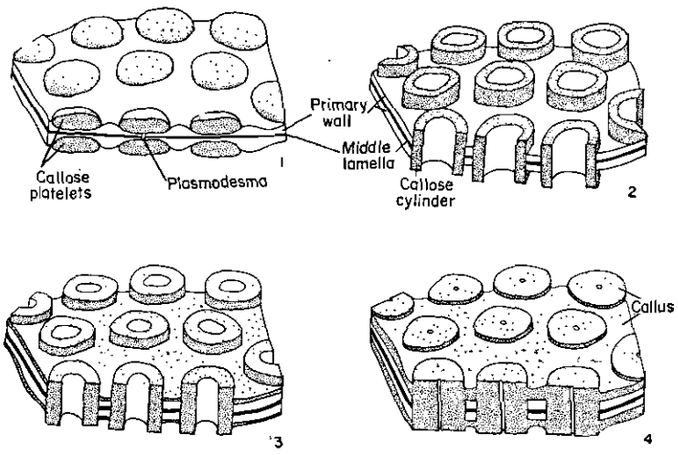

FIG. 48. Diagrams showing development and maturation of a portion of a sieve plate. 1, Early stage showing appearance of callose platelets. 2, The pores are lined by relatively thin callose cylinders. 3, The callose cylinders have thickened and callose has been deposited on the surface of the plate between the cylinders. 4, Sieve plate with definitive callus.

the pores varies in the different species from a fraction of a micron to 14 μ. In *Spiraea vanhouttei* the diameter of the pores is less than 1 μ while in *Pyrus malus* and *Pyrus communis* the maximum diameter is only a little larger than 1 μ, in *Curcubita* spp. it is 10·3 μ and in *Ailanthus altissima*, 14·3 μ (Esau and Cheadle, 1959). The presence of callose can easily be demonstrated by staining with aniline blue or resorcin blue (Esau, 1948). In ultraviolet light even minute amounts of callose stained with aniline blue give a lemon-yellow fluorescence. Callose also occurs on the walls of fungal cells, in the germination tube of pollen grains, in cystoliths, and recently, has even been shown to be present in the primary pit fields of epidermal cells (Currier and Strugger, 1956).

Callose is a polysaccharide built of D-glucose residues (Frey-Wyssling *et al.*, 1957). More accurate analysis has shown that in *Vitis* the callose

consists of β-D-glucopyranose residues with 1:3 linkages (Aspinall and Kessler, 1957). Callose is also found on those portions of the wall between the callose cylinders surrounding the connecting strands. In old elements large amounts of callose accumulate to form continuous thick layers which were termed *callus* by Hanstein in 1864. This term callus should not be confused with that referring to wound tissue.

In sieve areas that are not highly specialized the connecting strands are extremely thin and are nearly indistinguishable from plasmodesmata. In highly specialized sieve areas the connecting strands are very thick and they stain intensely. When the sieve element is young, the sieve area is thinner than the other portions of the cell wall and it appears as a depression on the inner surface of the wall. As the element matures additional callose is laid down not only on the cylinders, which line the pores, but also on the surface of the sieve area between the pores, so that finally, in old elements, the sieve areas do not appear as depressions but as raised portions above the surface. When the element ceases to function the connecting strands become very thin and may even disappear. When sieve areas develop close to one another the callose masses from each sieve area may fuse to form a single mass. Large masses of callose which develop with the cessation of function of the elements are called *definitive callus* (Fig. 49, no. 1). Usually, with the complete disintegration of the protoplast of the element the callus peels away from the sieve areas. In most dicotyledons the sieve elements function during a single growing season, but in certain plants, such as *Suaeda*, *Tilia* and *Vitis*, the sieve elements function for two or more years. In *Tilia* no distinct changes can be seen in the sieve elements with the start of the resting season, while in *Vitis* large amounts of callus accumulate in the autumn, disintegrate in the spring before the commencement of cambial activity, and so the sieve elements start to function for a second year (Esau, 1948; Bernstein and Fahn, 1960).

The density and arrangement of the sieve areas on the sieve elements exhibit the same degree of variation as does the pitting on the walls of the tracheary elements. On the basis of the thickness of the connecting strands and the degree of development of the callose cylinders, sieve areas with different stages of specialization can be distinguished. In certain plants, such as the Coniferales, all the sieve areas of an element are equal, while in other plants, for instance, most of the angiosperms, some of the sieve areas are more specialized, i.e. they have more well-developed connecting strands and callose cylinders than those found in other areas. These more specialized sieve areas are usually situated on the end walls of the elements which are horizontal or oblique to the longitudinal axis of the element. Those parts of the cell wall that bear such specialized sieve areas are called *sieve plates* (Fig. 49, no. 3).

Two theories exist as to the manner in which the pores of the si ve plate develop. According to one theorv the sieve plates develop fromeprimary

pit fields and then the connecting strands are derived from a single or a group of plasmodesmata. According to the second theory the pore sites of the future sieve plates contain no plasmodesmata and the formation of the pores involves the dissolution of the wall at the pore site.

According to Esau *et al.* (1962), the sites of the future pores are first delimited by the appearance of small deposits of callose in the form of

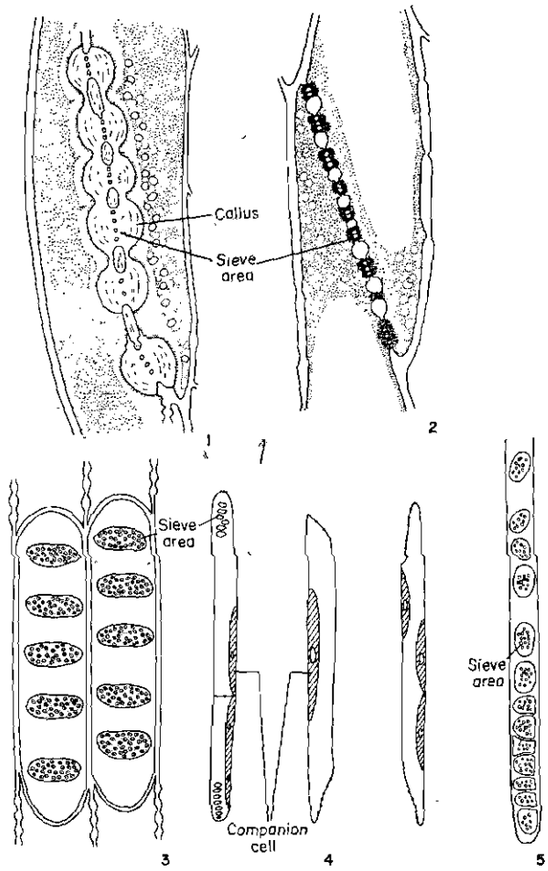

FIG. 49. 1–4, Sieve-tube members of *Vitis*. 1 and 2, Longitudinal sections of compound sieve plates between two elements. 1, Elements in dormant state in which the plate is covered by a thick layer of callus. 2, Elements reactivated after the removal of the callus. The slime which fills the sieve areas is indicated by heavy stippling. 3, Surface view of two compound sieve plates. 4, Sieve-tube elements with companion cells. 5, Portion of a sieve cell of *Pinus*. (Nos. 1–4, adapted from Esau, 1948.)

platelets. Apparently, the formation of the callose platelets takes place after the endoplasmic reticulum approaches the developing sieve plate. The callose platelets are paired and the two members of such a pair occur on the opposite sides of a sieve plate where they are separated from each other by thin portions of the wall consisting of the middle lamella and parts of the primary walls of the two adjacent cells (Fig. 48, no. 1). The

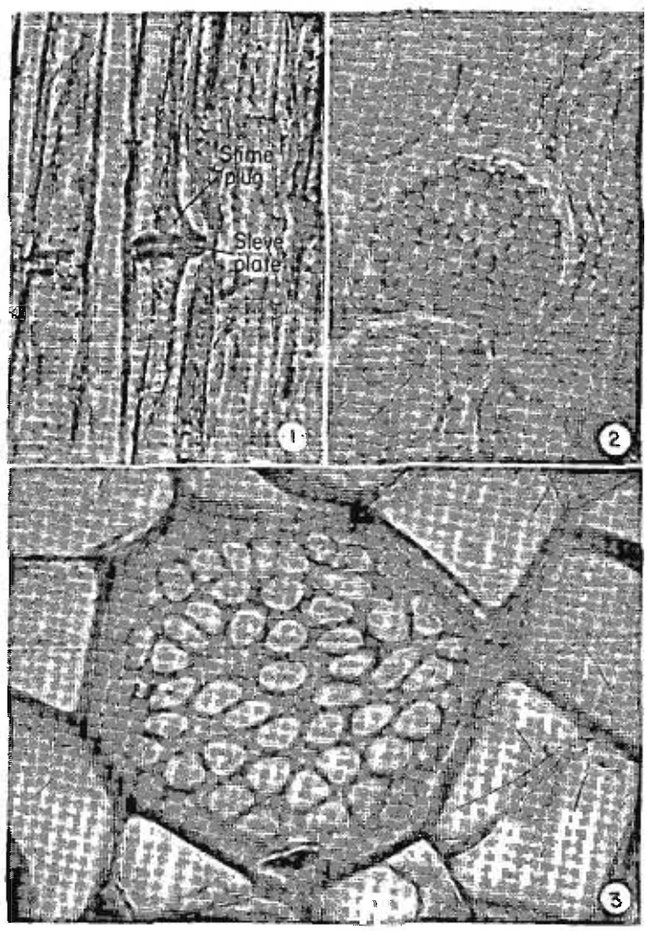

FIG. 50. 1, Micrograph of a longitudinal section in phloem of *Cucurbita*, stained with aniline blue, in which slime plugs can be distinguished. ×440. 2, Surface view of a sieve plate showing the pores lined by cylinders of callose; stained with aniline blue. ×640. 3, Surface view of a sieve plate showing the large pores; stained with safranin-fast green. ×880.

platelets increase in diameter, whereas the cellulosic bars between the pore sites decrease in width. These cellulosic bars together form the basic network of the sieve plate. The platelets and the bars increase in thickness. It appears that there is a single plasmodesma in each pore site. The perforation occurs in the centre of each platelet in that position where the thin wall dissolves. The callose platelets of each pair fuse around the perforation and thus each pore is lined with callose from its inception. Later, callose appears also on the surface of the sieve plate. The perforation of the sieve plate takes place after the disintegration of the nucleus.

Those sieve elements that have unspecialized sieve areas that are similar throughout the element are called *sieve cells* (Fig. 49, no. 5). Sieve cells,

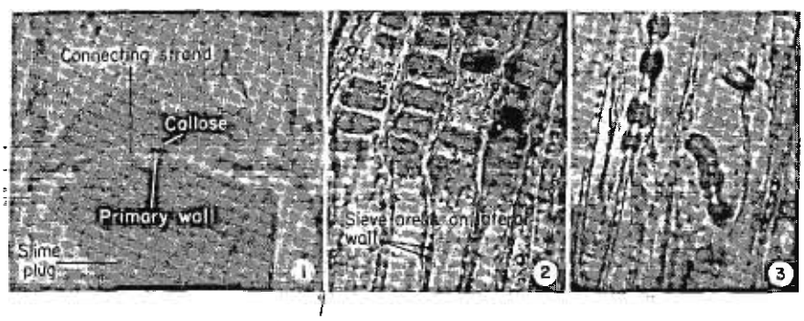

FIG. 51. 1, Cross-section of a sieve plate of *Cucurbita*. ×1200. 2 and 3, Compound sieve plates in secondary phloem of *Vitis*. 2, Surface view as seen in radial longitudinal sections of phloem. ×265. 3, Cross-section of plate as seen in tangential longitudinal section of phloem. ×265.

therefore, do not contain sieve plates. These cells are usually elongated with tapering ends or their end walls are very oblique. In the positions where sieve cells overlap one another the sieve areas are more numerous.

Elements in which sieve plates can be distinguished are called *sieve-tube members* (Fig. 49, no. 4). Sieve plates are usually found on the end walls which may be very oblique or horizontal or in intermediate planes. In certain elements, e.g. those of *Vitis* and *Pyrus malus*, the sieve plate contains several sieve areas; while in other elements, e.g. those of *Cucurbita*, only one sieve area may be present. The former type of sieve plate is termed a *compound sieve plate* (Fig. 49, nos. 1–4; Fig. 51, nos. 2, 3) and the latter, a *simple sieve plate* (Fig. 50, nos. 1–3). The sieve-tube members are connected one to the other by the walls that contain the sieve plates and so form *sieve tubes*. Sieve plates are found only very occasionally on the longitudinal walls of the sieve-tube members. On these walls unspecialized sieve areas develop.

THE CELL WALL

The walls of sieve elements are usually only primary and consist mainly of cellulose. Only in a single family of the Coniferales, the Pinaceae, has a secondary, non-lignified cell wall been found in the sieve cells (Abbe and Crafts, 1939). The thickness of the wall of the sieve elements varies in different species; in some species the cell wall is 1 μ thick while in other species the wall nearly fills the cell lumen. Esau and Cheadle (1958) also found differences in the structure of the wall. In certain species they found that the wall is homogeneous, while in others the wall is composed of two layers—a thin layer close to the middle lamella and a thicker layer next to the cytoplasm. The inner layer as seen in cross-sections of fresh material has a sheen similar to mother-of-pearl, and therefore has been termed the *nacreous* layer. The thickness of the wall of the sieve elements usually decreases with the aging of the element. Thick nacreous walls can be seen, for example, in *Magnolia*, *Laurus*, *Rhamnus* and *Persea* but they are not present in *Casuarina*, *Crataegus*, *Fraxinus*, *Morus*, *Populus*, *Salix* and *Passiflora*, among others.

THE PROTOPLAST

The most characteristic feature of the protoplast of the sieve element is the absence of a nucleus in the mature, active cell. The structure of immature sieve elements resembles that of the procambial and cambial cells from which they develop. In this stage the protoplast contains vacuoles and a large nucleus. With the specialization of the element the nucleus disintegrates and disappears. In certain plants the nucleolus or nucleoli are extruded from the nucleus prior to its disintegration and they remain within the sieve element.

A more or less viscous substance, which stains readily with cytoplasmic stains, is present in the sieve-tube members of dicotyledons. This substance has been termed *slime*. It is thought that slime is of a proteinaceous nature. It is located in the vacoule and in the preparation of sections it accumulates at the ends of the cells near the sieve plates. These slime accumulations are termed *slime plugs* (Fig. 50, no. 1; Fig. 51, no.1). The slime is produced in the cytoplasm in the form of small, variously shaped slime bodies that, with the specialization of the sieve element, become more liquid and pass into the vacuole where they become amorphous. This process takes place at the same time as the disintegration of the nucleus. In monocotyledons, gymnosperms and pteridophytes slime bodies have not been observed, and in these plants the vacuole of the sieve elements is aqueous with only small quantities of slime.

In the sieve elements of many species small plastids that take part in the synthesis of carbohydrate granules are present. These granules are similar to starch but stain red with iodine, and apparently contain a high

percentage of dextrins. In sections these granules accumulate, together with the slime, near the sieve areas.

It is difficult to get an accurate picture of the structure of the protoplast in a mature sieve element from the study of microscope sections because of the changes in position of the protoplasmic constituents that take place during sectioning. The cell contents are pushed in the direction of the cuts, and a portion may even be extruded onto the surface of the section by a pressure that exists in the mature sieve element. Under the microscope it is seen that the slime content of the vacuoles accumulates near those sieve areas close to the cuts and it appears as if this substance passes through the sieve areas. In order to avoid these artifacts investigators have used special fixation and other methods prior to sectioning.

The accepted view today is that there is a thin cytoplasmic layer lining the inner surface of the cell wall and the centre of the cell is occupied by a large central vacoule which contains the cell sap and different quantities of slime. The protoplasts devoid of nuclei are firmly attached to the sieve areas by the connecting strands (Esau, 1950). During the maturation of the sieve element the border between the vacuole and the cytoplasm disappears. From electron microscope studies it has been seen, during the nuclear disintegration, that the other organelles, the endoplasmic reticulum and the tonoplast become more or less disorganized. The plasmalemma and the remnants of the other cytoplasmic structures constitute the thin parietal cytoplasmic layer of the mature element (Esau and Cheadle, 1962). These and other features indicate reduced metabolic activity in the mature sieve elements.

Different opinions exist as to the nature of the connecting strands. According to one opinion these strands are entirely cytoplasmic, while according to another they contain vacuolar substances which serve as the connection between the vacuoles of the neighbouring elements. The latter view, i.e. that of vacuolar continuity, is the more accepted one today.

Different and contrary theories also exist as to the method of conduction of the photosynthetic products in the sieve elements (Esau *et al.*, 1957). According to one theory these substances are conducted through the sieve elements by a *mass flow* which is the result of the differences in hydrostatic pressure between the supplying and receiving organs. This theory was first formulated by Münch in 1930 and can be demonstrated by the following model. When an osmotic cell containing solutes is placed in water, water enters into it. The level of the solution in the osmometer will rise until equilibrium is reached between the hydrostatic and osmotic pressures. If two osmometers with solutions of different osmotic pressures are used, it is seen that the solution rises less in that osmometer with the lower osmotic pressure. If the two osmometers are connected there will be a flow from that osmometer with the higher osmotic pressure to that with the lower. This flow is a result of the pressure gradient between the two

osmometers. In the above case, molecules of solute flow passively with the solvent. Therefore, according to the theory of mass flow, the molecules of sugar and other dissolved substances are conducted through the phloem as a result of the flow of the aqueous solution. Thus the force, which enables the flow, is a result of the differences in the osmotic pressure between the supplying organs (the leaves) and the receiving organs (the roots, tubers, etc.). Supporters of this theory regard the phloem as the tube that connects the above-mentioned osmometers, as the cytoplasm in these elements, contrary to that of other cells, is permeable to the products of photosynthesis (Huber, 1941). According to these investigators the cytoplasm of the sieve elements lacks a tonoplast, is incapable of accumulating "neutral red" and does not plasmolyse when the cells are placed in a hypertonic solution.

Another theory is that of the active transport of the solutes. The supporters of this theory are of the opinion that the cytoplasm of the sieve elements takes an active part in the transfer of the substances. They suggest that the protoplasts of the sieve elements have the property of selective permeability, and they explain the difficulty of demonstrating plasmolysis of these cells by the particular sensitivity of the nucleus-free protoplast which therefore necessarily demands extremely careful treatment (Rouschal, 1941).

It is accepted by all workers that the passage of photosynthates in the sieve elements is much faster than that in ordinary parenchyma cells.

Phylogeny of sieve elements

In the most primitive form the sieve elements are parenchyma cells that have undergone modifications in connection with their function. This was followed by the loss of the nucleus. This protoplasmic specialization apparently resulted in the development of the interdependence of the sieve elements and parenchyma cells that retain their nucleus, i.e. the albuminous cells in the gymnosperms and the companion cells in the angiosperms. In the angiosperms the sieve elements and companion cells develop from the same mother cell. The specialization of the sieve elements also involved the development of thick connecting strands. In pteridophytes and gymosperms these strands are thin and resemble plasmodesmata, while in the angiosperms they are thick and conspicuous. The evolutionary trends in the shape of the sieve elements and the arrangement of sieve areas have been more thoroughly studied in the monocotyledons (Cheadle and Whitford, 1941; Cheadle, 1948; Cheadle and Uhl, 1948). The specialization, in this group of plants, has taken the following courses: (1) gradual localization of highly specialized sieve areas to the end walls of the elements; (2) gradual changes in the position of the end wall from very

oblique to horizontal; (3) gradual change from compound sieve plates to simple ones; (4) gradual reduction of the sieve-areas on the side-walls of the elements. In monocotyledons the above investigators also found that the sieve tubes first developed in the aerial portions of the plants from where the development and specialization spread to the roots. This direction of development is opposite to that of the development of the vessels in the xylem. This phenomenon is understandable from a functional point of view. Features of the dicotyledonous sieve-tube members suggest that the phylogenetic development in this group of plants is similar to that of the monocotyledons, but as yet no conclusive research has been done. According to Zahur (1959), the sieve-tube elements in the angiosperms, like the vessel elements, have undergone a decrease in length during the course of evolution.

Companion and albuminous cells

Sieve-tube members of the angiosperms are accompained by highly specialized parenchyma cells which are termed *companion cells* (Fig. 49, no. 4). These cells retain the nuclei throughout their life. The above two types of elements, i.e. the sieve-tube members and the companion cells, are related ontogenetically as they develop from the same meristematic cell. Such a meristematic cell divides longitudinally once or several times and one of the resulting cells, usually the largest, specializes to form the sieve-tube member and the others develop directly or indirectly, by further transverse or longitudinal divisions, into the companion cells. One or more companion cells may accompany a sieve-tube member. Companion cells vary in size—they may be as long as the sieve-tube member to which they are related or they may be shorter. Companion cells may develop on various sides of the sieve tube or they may form longitudinal rows on one side only. Companion cells are strongly attached to the sieve-tube members from which they usually cannot be separated even by maceration. The walls between sieve-tube members and the companion cells are thin or possess many thin areas which, apparently, are sieve areas on the side of the sieve-tube member and primary pit fields on the side of the companion cell. The length of life of the companion cells is usually the same as that of the sieve-tube member to which they are attached. This feature proves not only the ontogenetic connection but also the functional connection that exists between these cells. The companion cells and also the phloem parenchyma play an important part in the maintenance of a pressure gradient in the sieve tubes (Esau, 1961).

The protoplast of mature companion cells stains more intensely than that of ordinary parenchyma cells. It is thought that this staining property is due to the presence of a substance similar to that of the slime of the sieve-

tube members. Esau (1947, 1948) found slime bodies in the companion cells of *Vitis* and observed that, with the dispersal of this slime, the protoplast stained more intensely.

Starch has not been found in companion cells.

In pteridophytes and gymnosperms companion cells, as described above, do not occur, but cells which stain intensely with cytoplasmic stains are present. These cells are apparently connected physiologically and morphologically to the sieve cells and have been termed *albuminous cells*. Ontogenetically these cells develop from the phloem parenchyma or from cells of the phloem rays. Albuminous cells do not contain starch during the period that the phloem is active, but they may store it during the rest period.

Protophloem and metaphloem

The primary phloem, as described previously, consists of protophloem nad metaphloem. The protophloem, together with protoxylem, constitutes the vascular tissue of the young elongating parts of the plant.

The description of phloem elements given above refers only to metaphloem and secondary phloem. Sieve areas cannot be distinguished in the protophloem elements of gymnosperms. In angiosperms there are sieve-tube members in the protophloem but, in may plants, there are no companion cells. These sieve-tube members are long and narrow, and sieve areas can be distinguished only with difficulty. The walls are somewhat thick and the cell contents stain only slightly. The sieve tubes of the protophloem are apparently active for a short period only. As the sieve-tube members have no nucleus they cannot divide and grow with the elongating organ and so they become obliterated by the surrounding cells. The remnants of these obliterated cells may completely disappear in time. In many dicotyledonous stems the parenchyma of the protophloem remains after the obliteration of the sieve-tube members, and then these cells become fibres. In leaves they form elongated collenchyma cells.

In contrast to those sieve elements of the protophloem which only function for a short period and which are early obliterated, the sieve elements of the metaphloem of the Pteridophyta and long-living monocotyledons, such as the Palmae, apparently function for many years.

When fibres occur in the primary phloem of dicotyledonous plants they are always restricted to the protophloem even in those cases where fibres develop later in the secondary phloem of the same plant.

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CHAPTER 9

LATICIFERS

LATEX, a viscous liquid, is known to occur in many angiosperms. This liquid may occur either in series of cells or in single long cells; both these specialized structures have been termed *laticifers*. However, latex may also occur in unspecialized parenchyma cells.

Latex is a suspension or, in certain cases, an emulsion, the chemical composition of which differs in the different species. Among the suspended material rubber particles $[(C_5H_8)n]$, waxes, resins, proteins, essential oils, mucilages, and in certain *Euphorbia* species, variously shaped starch grains can be found. Latex, like the cell sap, also contains salts, organic acids and other substances in true solution. Certain plants contain, in the latex, sugars (the Compositae), tannins (*Musa*), alkaloids (*Papaver somniferum*), and in *Carica papaya*, a proteolytic enzyme, papaine, is present. The colour of latex varies in the different plant species—it may be white and milky (*Euphorbia*, *Lactuca*, *Asclepias*), yellow-brown (*Cannabis*), yellow to orange (*Papaver*) or colourless (*Morus*).

The function of the latex in the plant is not clear. Haberlandt (1918) believed the latex to be of nutritional value in many plants. Sperlich (1939) regarded latex as a reserve material. The most acceptable theory is that the latex contains metabolic by-products and the laticifers represent a secretory system. Substances that are regarded as excretory, rather than as reserve materials, accumulate in the laticifers. Rubber, for example, like the essential oils and unlike starch, cannot revert to nutritional substrates as no enzymes capable of breaking down rubber are present in the plant (Bonner and Galston, 1947). In the laticifers latex is under pressure and therefore when the laticifers are cut the latex is extruded. This is a pressure flow. The dynamics of latex flow have been dealt with in detail by Frey-Wyssling (1952).

The cell wall of the laticifers is entirely primary, and may be as thick as or thicker than the neighbouring parenchyma cells. Primary pit fields are rare in laticifers. In *Hevea* callose plugs have been found in the laticifers at the base of old leaves (Spencer, 1939).

Types of laticifers

According to De Bary (1877), the laticifers are divided into two main types: *non-articulated* and *articulated.* This classification has no relationship to taxonomic groups and thus different types of laticifers may be found in different species of one family.

The non-articulated laticifers develop from a single cell which greatly elongates with the growth of the plant and which is sometimes branched. Such laticifers are also termed laticiferous cells. Articulated laticifers consist of simple or branched series of cells which are usually elongated. The end walls of such cells remain entire or become porous or disappear completely. Such laticifers are also termed laticiferous vessels.

NON-ARTICULATED LATICIFERS

Non-articulated laticifers are characteristic of various species of the following families: Apocynaceae, Asclepiadaceae, Euphorbiaceae, Moraceae, and Urticaceae. Simple (unbranched) non-articulated laticifers are found, for example, in *Vinca*, *Urtica* and *Cannabis*, and branched non-articulated laticifers in *Euphorbia*, *Nerium*, (Fig. 53, nos. 1, 2) *Ficus* and *Asclepias.*

As has already been mentioned, different forms of non-articulated laticifers exist and in certain mature plants laticiferous cells may develop into very large systems which extend throughout the different shoot and root tissues. Schartfstein (1932) found that in some *Euphorbia* species the entire system is derived from a few initials that are already present in the embryo. Mahlberg (1961) found in *Nerium* that the number of initials is constant and that they can all be distinguished already in the embryo where they appear in the cotyledonary node from where they send branches into the cotyledons, the hypocotyl and the radicle (Fig. 53, nos. 1, 2). In the course of development of certain species of *Euphorbia* laticiferous cells are found on the circumference of the central cylinder and they branch into the leaves and pith. In the leaves of certain species of the Euphorbiaceae the laticiferous cells reach the epidermis where they may even come into contact with the cuticle. Blaser (1945) working on *Cryptostegia grandiflora* (Asclepiadaceae) found that the early-formed laticiferous cells in the cortex branch radially in the position of the leaf-gaps and penetrate into the pith. After a period of cambial activity these branches of the laticiferous cells become surrounded by the secondary phloem and xylem. The growth and expansion of the branched laticiferous cells is continuous throughout the life of the plant and their ends penetrate into the new buds, developing leaves and growing regions of the root. Such development of laticiferous cells, for example, has been observed in *Nerium* (Mahlberg, 1963).

The growth of these branched laticiferous cells is by a combination of intrusive and symplastic growth (Mahlberg, 1959b). It is of interest that, in certain plants, even the old portions of these cell walls retain the ability to grow and produce new branches as was shown by grafting experiments carried out by Scharffstein on *Euphorbia esculenta*. Numerous nuclei have been observed in the branched non-articulated laticifers of different plants. Scharffstein (1932) and Mahlberg (1959a) drew attention to the fact that the multiplication of the nuclei takes place early in the ontogeny of the laticiferous cell.

The growth of the simple non-articulated laticifers is simpler than that of the branched non-articulated ones. The initials of the former have not been observed in the embryo but only in the developing shoot, as, for instance, in *Vinca* and *Cannabis* (Zander, 1928; Scharffstein, 1932). The initials appear below the apical meristem and they develop into long, unbranched ducts which grow by a combination of intrusive and symplastic growth. These laticiferous cells may penetrate from the stem into the leaves (*Vinca*) or they may develop independently in these organs (*Cannabis*). In certain species multiplication of the nuclei also takes place during the development of simple non-articulated laticifers.

ARTICULATED LATICIFERS

Articulated laticifers are characteristic of different species of the Compositae, Convolvulaceae, Papaveraceae, Euphorbiaceae, Caricaceae, Sapotaceae, Liliaceae and Musaceae.

Simple (unbranched) articulated laticifers occur in Musa (Fig. 54, nos. 1–3), *Allium* (Fig. 52, no. 2), *Convolvulus* and *Ipomoea*. Branched articulated laticifers are found in *Sonchus* (Fig. 52, no. 1), *Cichorium*, *Lactuca*, *Taraxacum*, *Tragopogon*, *Scorzonera*, *Carica*, *Manihot* and *Hevea*. Like the non-articulated laticifers, the articulated laticifers appear in the early ontogenetic stages. In *Taraxacum kok-saghyz* the differentiation of the laticifers commences with the uptake of water at the time of the germination of the seed. The primary laticifers appear in the pericycle in close connection with the phloem, whereas the secondary laticifers differentiate in the secondary phloem very close to the cambium (Rudenskaja, 1938; Artschwager and McGuire, 1943; Krotkov, 1945). Scharffstein (1932), Sperlich (1939), Artschwager and McGuire (1943) and other workers observed the process of the formation of the articulated laticifers from single cells in the embryos of *Tragopogon*, *Scorzonera*, *Taraxacum* and *Hevea brasiliensis*. Articulated laticiferous vessels develop in many plants in the phloem or pericycle of the stem and root. They also occur in the leaf mesophyll. Apart from the connections formed between the cells of one laticifer by the entire or partial dissolution of the end walls, connection

may also be made between adjacent laticiferous vessels in species with branched articulated laticifers. Articulated laticifers may also become connected by horizontally or diagonally orientated elements. Reticulate systems may also develop as a result of the formation of branches which arise on the side walls of the laticifers. Sometimes parenchyma cells between two laticiferous vessels redifferentiate and so connect the two vessels.

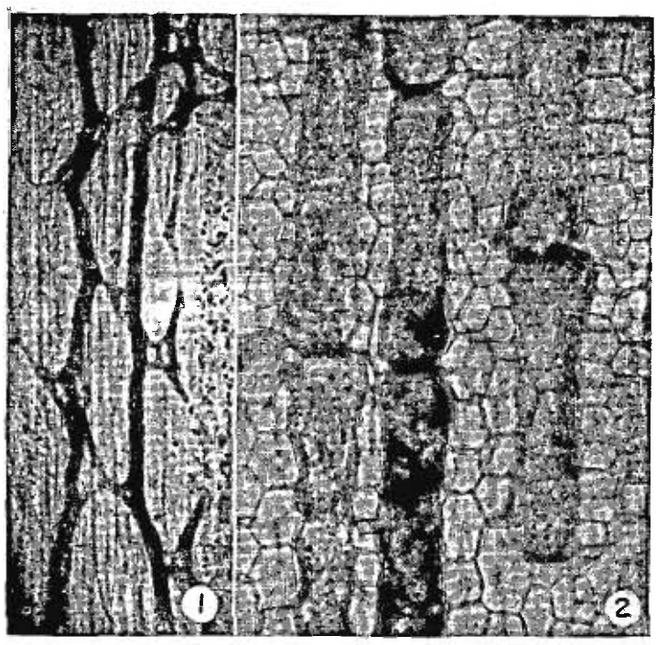

FIG. 52. 1, Micrograph of a stem of *Sonchus oleraceus*, cleared with lactic acid, to show the branched, articulated laticifers. × 140. 2, Tangential section at a depth of two cells below the abaxial epidermis of a bulb scale of *Allium cepa* in which simple articulated laticifers can be distinguished. ×115.

The simple (unbranched) laticifers of *Musa* usually accompany the vascular tissues (Skutch, 1932). In *Musa* the central portion of the end walls of two adjacent cells becomes torn away, but usually it remains attached to one side of the cell where it appears as a loose flap (Fig. 54, nos. 2, 3). In *Allium* the laticiferous vessels are in no way connected with the vascular tissue and they are found in the third layer of leaf mesophyll or in the third layer below the abaxial epidermis of the bulb scales. The end walls of the cells of the laticifers of *Allium* are not perforated, but well developed primary pit fields appear in them.

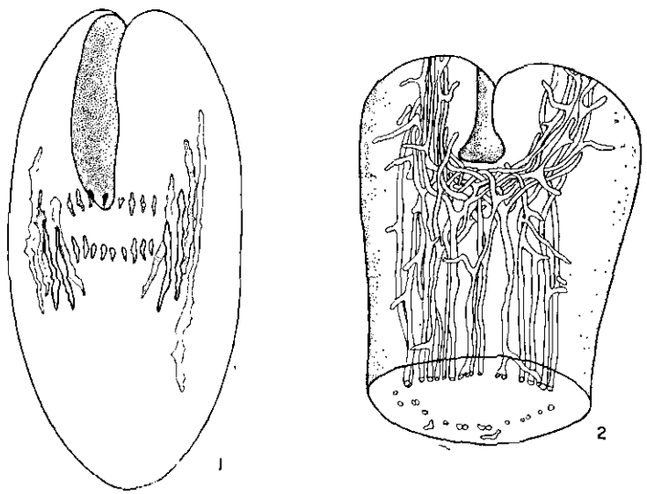

FIG. 53. 1, Reconstruction of 28 laticifer initials in the cotyledonary node of an immature embryo (550 μ long) of *Nerium oleander*. The initials are situated on the periphery of the provascular system. 2, As above, but cotyledonary node of a mature embryo (5 mm long). (Adapted from Mahlberg, 1961.)

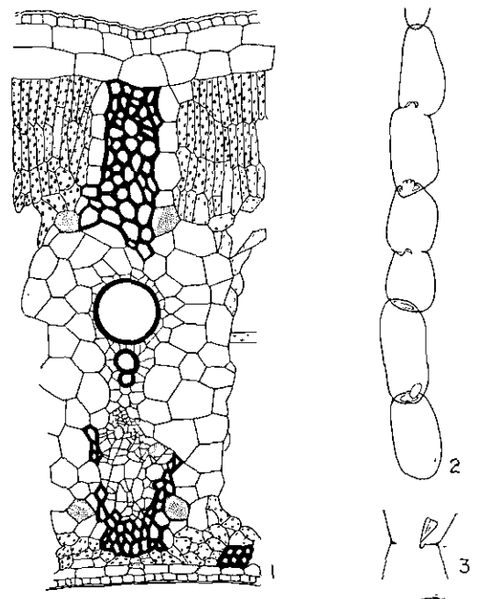

FIG. 54. Laticifers in *Musa*. 1, Portion of a cross-section of a leaf showing laticifers accompaning the vascular bundle. Laticifers, stippled. 2, Diagram of a portion of laticifer showing the articulation. 3, Diagram showing opening and flap between two adjacent cells of the laticifer.

RUBBER PLANTS

There are many plant species from which rubber can be obtained, but of them, *Hevea brasiliensis* in the Euphorbiaceae, which is known as the Para rubber tree, is the most important in world economics. This plant is today grown in central America, the West Indies, Brazil, Liberia, Ceylon, Malayan Archipelago, Sumatra, Java and eastern India. The latex of *H. brasiliensis* contains about 30% rubber.

Other rubber plants of secondary economic importance (Schery, 1954) are *Castilla* (Panama rubber) in the Moraceae, *Manihot* (Ceara rubber) in the Euphorbiaceae, *Parthenium argentatum* (guayule) and *Taraxacum kok-saghyz* in the Compositae, *Hancornia* and *Landolphia* in the Apocynaceae, and *Cryptostegia* in the Asclepiadaceae. *Parthenium argentatum* was investigated thoroughly in the U.S.A., during World War II, when rubber was unobtainable from the *Hevea* plantations in Asia.

The analogy in the structural organization of the laticifers with that of the vascular system is of interest. On this basis, the non-articulated laticifers can be compared to tracheids and sieve cells. However, laticifers, which have no conducting function, do not necessarily have to be mature throughout their entire length and so their ends can grow continuously at the plant apices. It is possible that if tracheids and sieve cells did not necessarily have to be of so specialized a structure in order to function soon after their initiation, they too would be capable of such extensive growth as is exhibited by these laticiferous cells. The articulated laticifers can be compared with vessels and sieve tubes as they are similarly built of series of many cells. This similarity was probably one of the reasons why early botanists considered the laticifers to be structures concerned with the conduction of nutrients.

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CHAPTER 10

EPIDERMIS

THE epidermis constitutes the outermost layer of cells of the leaves, floral parts, fruits and seeds, and of stems and roots before they undergo considerable secondary thickening. Functionally and morphologically the epidermal cells are not uniform and among them, apart from the ordinary cells, many types of hairs, stomatal guard cells, and other specialized cells are found. Topographically, however, and to a certain extent also ontogenetically, the epidermis constitutes a uniform tissue.

The earliest stages of the ontogenetic development of the epidermis differ in the root and shoot (see Chapter 3). This fact caused certain investigators to coin special terms, *epiblem* and *rhizodermis*, for the outermost layer of the root (Linsbauer, 1930; Guttenberg, 1940, and others). However, if the development of the epidermis from the protoderm is traced ignoring the problem of the origin of this meristematic tissue, it is possible to apply the term *epidermis* to all the organs of the various groups of vascular plants.

The epidermis usually exists throughout the entire life of those organs that have no secondary thickening. In a few plants, such as long-lived monocotyledons with no secondary thickening, the epidermis is replaced by a cork tissues as the organs age. The duration of the epidermis in organs with secondary growth differs; usually in stems and roots the epidermis is replaced by the periderm during the plant's first year, but there are certain trees, e.g. *Acer striatum*, in which the periderm develops only after several years of secondary growth of the organ (De Bary, 1877). In such cases the epidermal cells continue to divide anticlinally and to enlarge tangentially (Fig. 148, nos. 3–6).

Uniseriate and multiseriate epidermis

In most spermatophytes the epidermis consists of a single layer of cells, but in certain plants one or several cell layers, which are morphologically and physiologically distinct from the inner ground tissue, are found on the inside of the surface layer. These layers may develop ontogenetically from two different meristematic tissues, i.e. from the meristem of the ground tissue or from the protoderm. In the former case, these layers

are termed a *hypodermis* and, in the latter case, the tissue formed is regarded as being a *multiseriate epidermis*. A multiseriate epidermis develops as a result of periclinal divisions of the protodermal cells. These divisions are relatively delayed and occur in late ontogenetic stages, e.g. in the leaves of *Ficus elastica* the epidermis remains single-layered till the stage

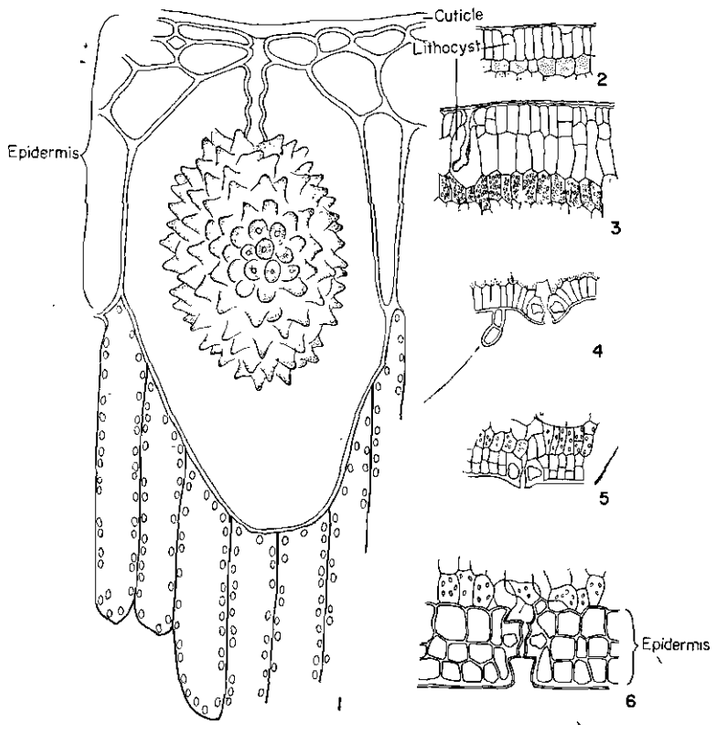

FIG. 55. Portions of cross-sections of the leaf blade of *Ficus elastica*. approx. ×500. 1, Adaxial side of the blade in which the multiseriate epidermis the cells of which include a lithocyst (a cystolith-containing cell), can be distinguished. 2 and 3, Two early stages in the development of the adaxial multiseriate epidermis and a lithocyst. 4–6, Stages in the development of the multiseriate abaxial epidermis. (Adapted from De Bary, 1877.)

when the leaf begins to expand in the bud and the stipules are shed (Fig. 55, nos. 1–6). Multiseriate epidermis occurs in the Moraceae, certain species of the Begoniaceae and Piperaceae, and some articulated Chenopodiaceae. In *Anabasis articulata* the multiseriate epidermis develops in the lower region of each internode (Fig. 63, nos. 1–6; Fig. 64, nos. 1, 2)

The *velamen*, the special absorbing tissue of orchid roots, is also a multiseriate epidermis (Fig. 67, nos. 3, 4). The cells of the innermost layer of the multiseriate epidermis of leaves usually function as a water-storing tissue (De Bary, 1877).

Epidermal cells

Various types of epidermal cells can be distinguished in different plants: the ordinary cells of the epidermis; single cells or groups of cells with special structure, form or content; cells connected with stomata; and epidermal appendages termed *trichomes*.

THE ORDINARY CELL OF THE EPIDERMIS

The ordinary cells of the epidermis vary in shape, size and arrangement, but they are always closely attached to form a compact layer devoid of intercellular spaces. In the epidermis of petals air spaces may sometimes occur but they are always covered by the cuticle (Eames and MacDaniels, 1947). Many epidermal cells are tabular, and in the leaf blade of dicotyledons the anticlinal walls are mostly sinuous. In the stems, and especially in the leaves of many monocotyledons, the epidermal cells are elongated. In the epidermis of certain seeds (in species of the Leguminosae and in *Punica*) the cells are relatively very elongated in a radial direction and are rod-shaped. In certain plants, for instance *Aloë aristata*, the epidermal cells appear to be hexagonal in surface view but actually they are polyhedral, and according to Matzke (1947), the average number of faces is 10·885. The external wall of the epidermal cells of certain leaves and petals is raised in the form of papillae. In certain pteridophytes such papillae are found on the epidermal cell wall facing the mesophyll.

Wall structure

The epidermal cell wall differs in thickness—some cells are thin-walled while in others the outer wall is thicker than the other walls. In seeds, scales and certain leaves, e.g. the leaves of conifers, the epidermal cell walls are very thick and lignified (Fig. 103, no. 2; Fig. 104, no. 2).

Primary pit fields are often found in the walls, especially on the radial and inner walls, of the epidermal cells. In the outer epidermal wall of many leaves plasmodesmata are present. These plasmodesmata are termed *ectodesmata* and they may have the appearance of ordinary plasmodesmata

dicum and *Helxine soleirolii*) or paintbrush-shaped (e.g. in the bulb scales of *Allium cepa*, the first leaves of *Antirrhinum majus* and the leaves of *Sidalcea neomexicana*). In both these cases the broad part of the ectodesma is directed toward the cell lumen (Franke, 1962). In the epidermal cells of certain leaves, petals and dry fruits, partial partitions are found on the inside of the outer wall. These partitions sometimes almost reach the inner epidermal wall (Fig. 205, no. 1).

Cutin, a fatty substance, is usually present in the outer walls of the epidermal cells. This substance is found within the cell wall, i.e. in the interfibrillar and intermicellar spaces of the cellulose, and it also constitutes a special layer—the *cuticle*—on the outer surface of the cell wall (Fig. 88, no. 1). Cutin stains red with Sudan IV. All the parts of the herbaceous stem, the leaves and, to a certain extent, the mature portions of the root are covered with a cuticle. The cuticle is usually absent from the actively growing parts of the roots. During the early stages of the development of the epidermis, the cuticle of each cell does not reach the margins of the cell (Loomis and Schieferstein, 1959) but later it forms a continuous layer which covers the entire epidermis.

In certain plants, which have been preserved from early geological eras, the cuticle has retained its shape and the structure of the epidermal cells can be learnt from it. These preserved fragments of cuticle are often used to classify these early plants (Fig. 58, no. 1).

The cuticle is of varying thickness in different plants, and it is usually thicker in plants growing in dry habitats (Fig. 88, no. 1). The surface of the cuticle may be smooth, rough, ridged or furrowed (Fig. 58, no. 2). Priestley (1943) states that very thin layers of cutin can be distinguished on those mesophyll cell walls that border the intercellular spaces. These spaces form a continuous system connected with the stomata and therefore these cutin layers constitute a continuation of the cuticle on the outer surface of the epidermis. The cuticle on the surface of the epidermis often penetrates, to a certain extent, between the radial walls of the epidermal cells (Fig. 104, no. 2). In the outer thick walls below the cuticle there are alternating lamellae of cellulose and pectic substances. Cutin is found in both these types of lamellae. Therefore we distinguish between the cuticle proper and the *cuticle layer* which is found below it. The cuticle proper is formed by the secretion of cutin or its precursors, i.e. by cuticularization (Fritz, 1935, 1937; Roelofsen, 1952). The cuticle layer is formed by the deposition of cutin in the intermicellar and interfibrillar spaces in the outermost cell wall layer, i.e. by cutinization. The cuticle layer consists of several lamellae—up to 20 in the leaves of *Aloë*, for instance, and up to 65 in the pericarp of *Asparagus*. The lamellar structure can be distinguished without any special treatment in *Eucalyptus* and *Viscum*. The outermost lamellae of the cuticle layer are very poor in cellulose but are rich in cutin and contain a large amount of pectin. The inner lamellae (greater

in number) contain more cellulose. In *Aloë* six lamellae rich in cutin were found to alternate with five lamellae rich in cellulose. Still further inwards, toward the cell lumen, the cuticle layer of *Aloë* contains several lamellae with an even lower cutin content, and which probably also differ in their pectin content. In the non-cutinized part of the wall the presence of pectin has been proved.

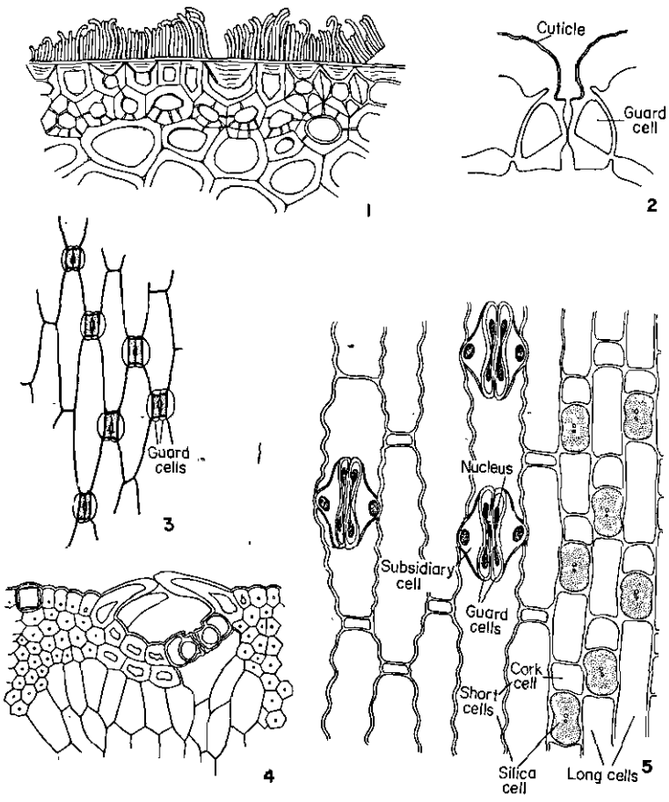

FIG. 56. 1, Portion of a cross-section of the stem of *Saccharum* showing rod-shaped or hair-like wax deposits on the surface of the epidermis. 2, Cross-section of a stoma of *Allium cepa*. 3, Surface view of the epidermis of *Iris* in which the stomata can be seen to be arranged in longitudinal rows. The stomata are sunken and the rectangular depressions formed by the overarching of the neighbouring epidermal cells are shown as shaded areas in the diagram. 4, Portion of a cross-section of the leaf of *Xanthorrhoea gracilis* in which a sunken stoma overarched by trichomes can be seen. 5, Surface view of the epidermis of *Pennisetum clandestinum* showing epidermal cells characteristic to the Gramineae. (No. 1, adapted from De Bary, 1877; no. 2, adapted from Haberlandt, 1918.)

The above structure of the cuticle suggests that the passage of the cutin is from the inside outwards and that it accumulates on the surface where it forms the cuticle.

Various theories have been proposed to explain this outward movement of the cutin. According to some investigators special channels are present in the outer epidermal walls through which the fatty substances, which form the cutin, pass (Scott *et al.*, 1957); other investigators believe that the porous nature of the wall suffices. The latter view is more acceptable.

Deposits of *wax* in the form of granules, as in *Brassica*, *Dianthus*, or of rods, as in *Saccharum* (Fig. 56, no. 1) or as continuous layers, as in *Thuja orientalis*, are often found on the surface of the cuticle. In the leaves of *Agave* a continuous layer of wax is also found below the cuticle (Schieferstein and Loomis, 1959). In certain plants platelets of wax have been found within the cutin of outer epidermal cell walls (Roelofsen, 1952). Deposits of salts in the form of crystals, e.g. in *Tamarix* and *Plumbago capensis*, of caoutchouc, e.g. *Eucalyptus*, or of oils and resins sometimes occur on the surface of cuticle or within it. Deposits of silicon salts are found in the epidermal cell walls of many plants, as, for example, *Equisetum*, the Gramineae, many species of the Cyperaceae, the Palmae and certain species of the Moraceae, the Aristolochiaceae and the Magnoliaceae (Metcalfe and Chalk, 1950).

Lignin is rarely found in the epidermal cell walls. When it is present it may be found in all the walls or only in the outer wall. Lignified epidermal walls are found in the leaves of the Cycadaceae, in the needles of conifers, the rhizomes of the Gramineae, in the strips of epidermis above the bundles of sclerenchyma in the leaves of the Gramineae, Juncaceae and Cyperaceae, in the leaves of certain species of *Eucalyptus* and *Quercus* and in *Laurus nobilis* and *Nerium oleander*.

Parts of the epidermal cell walls of groups of cells or of single cells may become mucilaginous in certain dicotyledonous families, such as the Moraceae, Malvaceae, Rhamnaceae, Thymelaeaceae and Euphorbiaceae. In certain seeds, such as those of *Linum usitatissimum* (Fig. 216, no. 2) and species of *Alyssum*, the outer walls of the epidermal cells become mucilaginous. In the nectaries of certain plants the epidermal cells also become mucilaginous at the time of nectar secretion (Fahn, 1952).

Protoplast

The protoplast of the epidermal cells of most plants contains minute leucoplasts and is devoid of chloroplasts. Chloroplasts are found in certain pteridophytes, hydrophytes and in some shade plants. Anthocyanins are found in the vacuoles of the epidermal cells of the petals of numerous

flowers, in the leaves of *Zebrina pendula* and red cabbage, in the stems and petioles of *Ricinus* and in different organs of many other plants. Tannins, mucilage and crystals may be present in epidermal cells.

EPIDERMAL CELLS WITH SPECIAL STRUCTURE OR CONTENT

In certain pteridophytes, in the gymnosperms, in many species of the Gramineae and certain dicotyledons fibre-like epidermal cells are found.

In the Gramineae, between the elongated epidermal cells, i.e. *long-cells*, above the veins, there are *short-cells* which are of two types—*silica-cells*

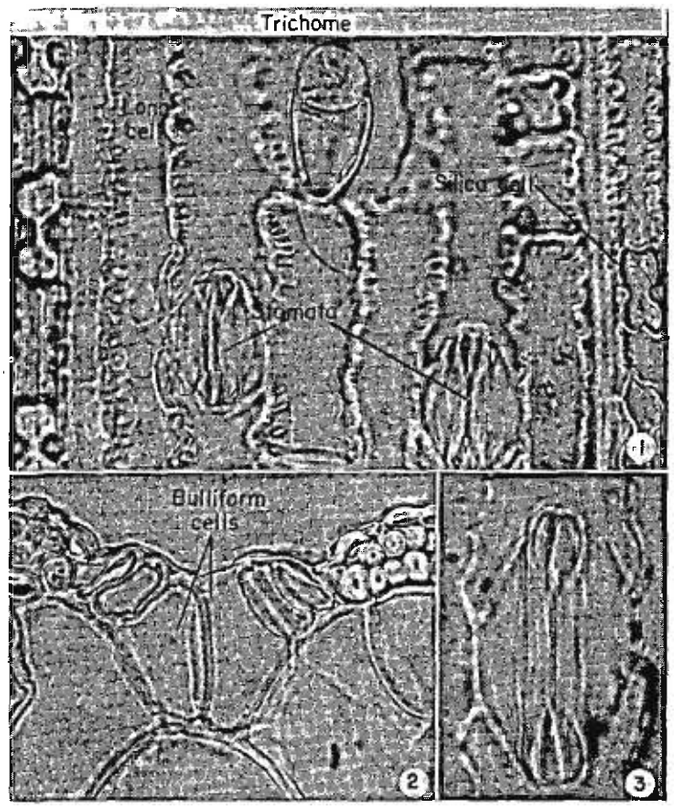

FIG. 57. 1, Surface view of the epidermis of a grass leaf *(Crypsis schoenoides)*. ×600. 2, Portion of a cross-section of a grass leaf *(Dactyloctenium robecchi)* in which bulliform cells can be distinguished in the epidermis. ×110. 3, Surface view of a stoma of *Crypsis schoenoides*. ×1000.

and *cork-cells*. The latter two types of cells often occur successively in pairs, throughout the length of the leaf. The silica-cells contain silica-bodies which are isotropic masses of silica in the centre of which are usually minute granules. In surface view the silica-bodies may be circular, elliptic, dumbbell or saddle-shaped (Fig. 56, no. 5; Fig. 57, no. 1). The walls of the cork-cells are impregnated with suberin and many of them contain solid organic substances. The above short-cells sometimes bear papillae, setae, spines or hairs. Metcalfe (1960) draws attention to the fact that the cork-cells in many plants contain silica-bodies, and that in certain grasses silica-bodies also occur in some elongated cells. Silica-bodies also occur in specialized epidermal cells of the Cyperaceae and some other monocotyledons (Metcalfe, 1963).

In the Gramineae and many other monocotyledons, with the exception of the Helobiae, *bulliform cells* are found in the epidermis. These cells are larger than the typical epidermal cells and they are thin-walled and have a large vacuole. The bulliform cells may constitute the entire adaxial epidermis of the leaf or they form isolated parallel strips in the area between the veins. In a cross-section of the leaf these cells appear in a fan-like arrangement in which the central cell is the tallest. In certain plants bulliform cells are also found on the abaxial surface of the leaf. These cells are sometimes accompanied by similar mesophyll cells. Bulliform cells contain much water and are devoid, or nearly so, of chloroplasts. Their wall consists of cellulose and pectic substances, and the outermost wall contains cutin and is covered by cuticle (Fig. 57, no. 2).

Different opinions exist as to the function of the bulliform cells. According to one opinion they function in the opening of the rolled leaf as present in the bud. According to a second view they bring about the rolling or unrolling of mature leaves as a result of their loss or uptake of water. Recent research carried out by Shields (1951) on twelve xerophytic grass species has questioned the importance of the bulliform cells in both the opening of the young leaves from the bud and in the hygrochastic movements (opening due to water absorption) of the matrue leaves. According to Metcalfe (1959), the bulliform cells often become filled with large masses of silica and their outer walls often become thick and cutinized.

Other specialized epidermal cells are the cystoliths which are found in the Acanthaceae, Moraceae, Urticaceae and Cucurbitaceae. In the Cruciferae *myrosin cells* are sometimes found in the epidermis. These cells are sac-like secretory cells which contain the enzyme myrosin, and they stain red in the Millon test, or violet with orcein solution and concentrated hydrochloric acid.

STOMATA

The continuity of the epidermis is interrupted by minute openings which are intercellular spaces each of which is limited by two specialized cells termed the *guard cells* (Fig. 58, no. 3). The guard cells together with the opening between them constitute the *stoma.* In many plants *subsidiary* or *accessory cells* can be distinguished. These cells differ morphologically from the typical epidermal cells and they constitute two or more cells bordering the guard cells to which they are apparently functionally connected (Fig. 58, no. 3). The subsidiary cells usually develop from protodermal cells adjacent to the stomatal mother cells but they may also develop from sister cells of the mother cell (De Bary, 1877).

Stomata are usually found on the aerial portions of the plant and especially on leaves, ordinary stems, and rhizomes. Stomata are absent from roots and the entire plant body of certain parasitic plants that lack chlorophyll, such as *Monotropa* and *Neottia.* In *Orobanche*, however, stomata are found on the stem although this genus is also devoid of chlorophyll. Stomata are present in some submerged water plants but not in most others. Stomata may be found on petals, staminal filaments (e.g. *Colchicum)*, carpels and seeds, but these stomata are usually non-functional.

In photosynthesizing leaves stomata may be found on both sides of the leaf or on the lower side only. In certain water plants with leaves that float on the surface of the water, e.g. *Nymphaea,* stomata are found only on the upper surface of the leaf which is exposed to the atmosphere. The number of stomata per square millimetre is different in different plants; for example, in *Pistacia palaestina* there are 176 stomata per square millimetre; in *Pistacia lentiscus,* 255; in *Styrax officinalis,* 261; in *Quercus calliprinos,* 402; and in *Olea europaea,* 545.

In leaves with reticulate venation the stomata are distributed in no particular order, while in leaves in which the majority of veins are parallel, as in the Gramineae, the stomata are arranged in parallel rows.

The guard cells of the stomata may be level, sunken (Fig. 56, no. 2) or raised relative to the other epidermal cells. In cases where the epidermis is multiseriate, e.g. as in species of *Anabasis* and *Haloxylon* and in *Ficus elastica*, the guard-cell mother cells are differentiated at that stage of development when the protoderm is as yet a single layer. During the process of further development the surrounding protodermal cells undergo several periclinal divisions resulting in the raising of the multiseriate epidermis above the level of the guard cells (Fig. 63, nos. 1–6; Fig. 64, nos. 1, 2) (Fahn and Dembo, 1964).

Below the stomata and directed inwards to the mesophyll are large intercellular spaces which are termed *substomatal chambers* (Fig. 103, no. 2).

The guard cells of most plants, except those of the Gramineae and Cyperaceae and some others, are kidney-shaped in outline. The size of the aper-

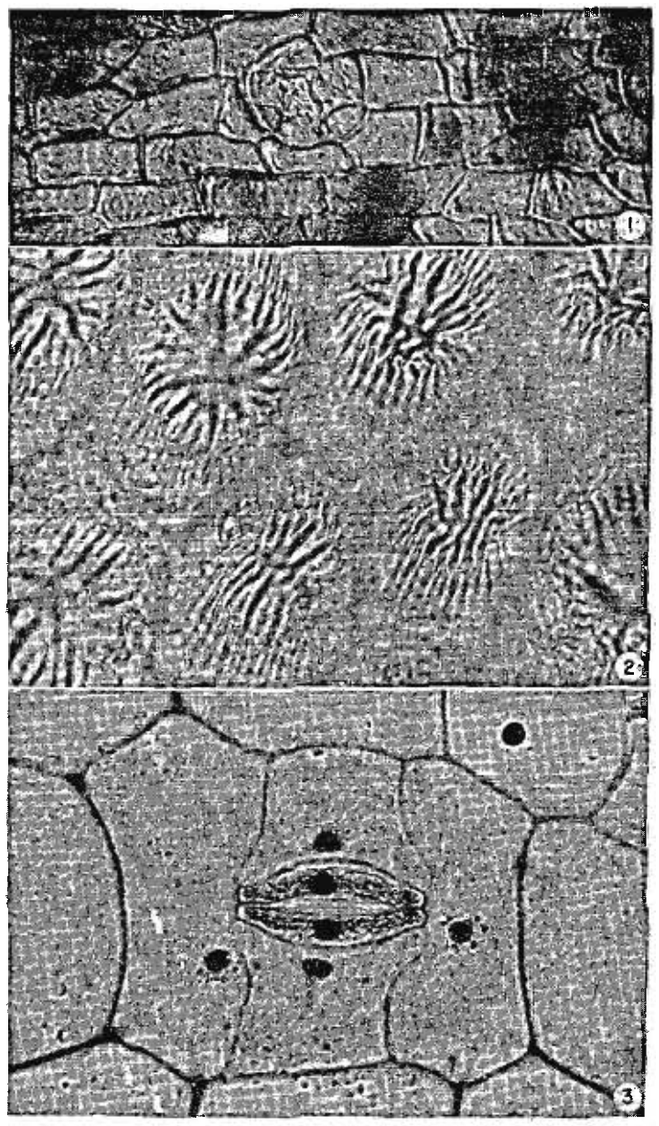

FIG. 58. 1, Micrograph of the cuticle of the fossil *Cupressinocladus* from which the shape of the epidermal cells can be determined. ×700. 2, Micrograph of a surface view of the abaxial epidermal cells in a region above a vein of a petal of *Pelargonium zonale;* it is possible to distinguish cuticular striations particularly in the central portion of the cells which is papillate. ×780. 3, Micrograph of a surface view of the abaxial epidermis of *Zebrina pendula* in which guard cells and subsidi-

ture between the guard cells increases or decreases as a result of turgor changes in the guard-cell vacuoles. The movements are possible because of the unequal thickness of the walls of the guard cells. This feature is particularly obvious in cross-sections, where the cell lumen usually appears triangular (Fig. 56, no. 2). In most cases the thinnest wall is that closest to the subsidiary or ordinary neighbouring epidermal cells; this wall is termed the *back wall*. The increase in turgor causes the cell sap to press against all the walls and results in the expansion of the walls and especially of the thin, more elastic back walls. The back walls stretch vertically and also

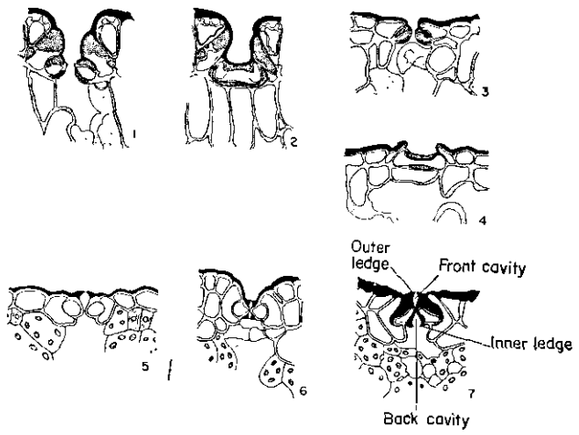

FIG. 59. Various types of stomata. 1 and 2, *Abies pinsapo*. 3 and 4, *Juniperus chinensis*. 5, *Syriechanthus fibrosus*. ×280. 6, *Corypha talieri*. ×175. 7, *Chamaerops humilis*. ×280. Nos. 2 and 4, longitudinal sections; the rest cross-sections. Cuticle represented by solid black, lignified areas by dark shading. (Nos. 1–4, adapted from Florin, 1931; nos. 5–7, adapted from Tomlinson, 1961.)

become somewhat convex and so push into the neighbouring epidermal cells. These walls thus draw apart the thick outer and inner walls, which are much less elastic and cannot stretch. Therefore the angle, which can be seen in cross-section at the junction of the outer and inner walls at the edge of the stomatal aperture, increases and the stomatal aperture is widened, i.e. opens. Protuberances of the guard-cell wall may be present above, or both above and below, the stomatal aperture (Fig. 59, no. 7). In cross-section these protuberances appear as horn-shaped ledges. The outer ledge delimits the front cavity above the aperture, and the inner ledge delimits the back cavity which abuts on the substomatal chamber.

The guard cells in the Gramineae and Cyperaceae are of a form different from that which has been described above. They are elongated and bone-shaped. The ends of these guard cells are expanded and thin-walled, while

the middle portions are elongated and thick walled and the cell lumen is narrow (Fig. 56, no. 5). As a result of turgor increase in this type of guard cell, the expanded tips swell and so push apart the middle elongated portions of the cells. Because of the above structure the nuclei in the guard cells of grasses appear as two ellipses connected by a narrow thread. According to Flint and Moreland (1946) the two parts of the nucleus may become completely separated.

The chemical composition of the guard-cell wall is the same as that of the ordinary epidermal cells of the same plant. They are usually covered by cuticle which generally continues on that wall that faces the aperture

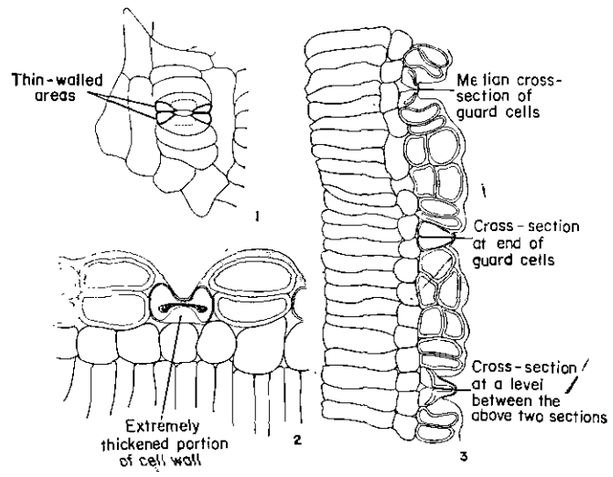

FIG. 60. Structure of stomata of *Haloxylon articulatum*. 1, Surface view showing thin-walled areas at the ends of the guard cells. 2, Portion of a cross-section of the stem, showing a guard cell in longitudinal section. The cell-lumen is dumb-bell shaped; nucleus heavily stippled. 3, Portion of longitudinal section of stem showing the biseriate epidermis and sunken stomata, sectioned transversely at various levels. ×400.

and it also reaches the cells abutting on the substomatal chamber. In *Citrus*, cuticle is absent from the cell wall facing the stomatal aperture (Turrell, 1947).

Apart from the types of guard-cell structure described above many other structural variations exist in the mono- and dicotyledons, e.g. in species of *Haloxylon* (Fig. 60, nos. 1–3) and *Anabasis* and in the Palmae (Fig. 59, nos. 5–7). These variations probably result in different methods of functioning (Tomlinson, 1961; Fahn and Dembo, 1964).

The various types of stomata in the Coniferales (Fig. 59, nos. 1–4) have been described by Florin (1931). He distinguishes several types accord-

ing to the movements of the guard cells during the opening of the stomata. These variations in movement are due to the different positions of the thin parts of the wall as well as to the presence and position of the lignified and non-lignified wall areas.

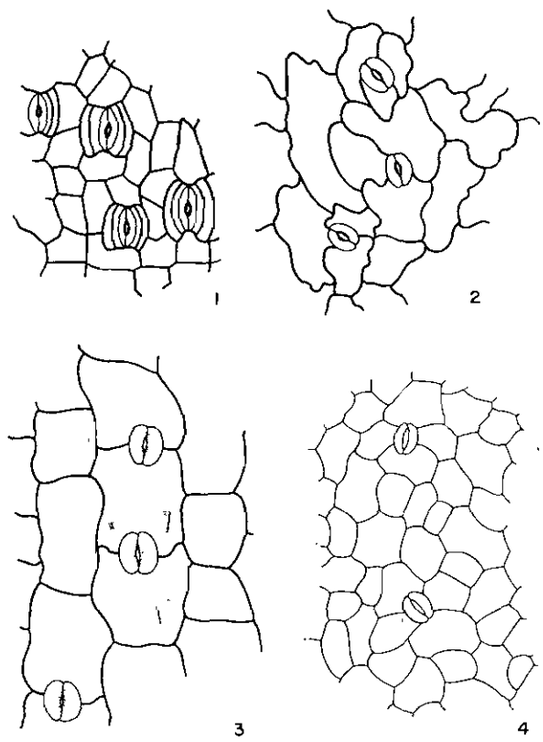

FIG. 61. Different types of arrangement, as seen in surface view of the leaf, of the subsidiary cells relative to the stoma. 1, *Acacia*; rubiaceous or paracytic type. 2, *Brassica*; cruciferous or anisocytic type. 3, *Dianthus*; caryophyllaceous or diacytic type. 4, *Pelargonium*; ranunculaceous or anomocytic type.

Morphologically, four main types of stomata have been distinguished in the dicotyledons, on the basis of the arrangement of the epidermal cells neighbouring the guard cells (Metcalfe and Chalk, 1950).

1. The *ranunculaceous* or *anomocytic type* (Fig. 61, no. 4) in which the guard cells are surrounded by a certain number of cells that do not differ in size and shape from the other epidermal cells. This type is common in the Ranunculaceae, Geraniaceae, Capparidaceae, Cucurbitaceae, Malvaceae, Scrophulariaceae, Tamaricaceae and Papaveraceae.

2. The *cruciferous* or *anisocytic type* (Fig. 61, no. 2) in which the guard cells are surrounded by three unequally-sized subsidiary cells. This type is common in the Cruciferae, in *Nicotiana, Solanum, Sedum* and others.

3. The *rubiaceous* or *paracytic type* (Fig. 61, no. 1) in which each guard cell is accompanied by one or more subsidiary cells, the longitudinal axes of which are parallel to that of the guard cells and aperture. This type is common in the Rubiaceae, Magnoliaceae, most species of the Convolvu-

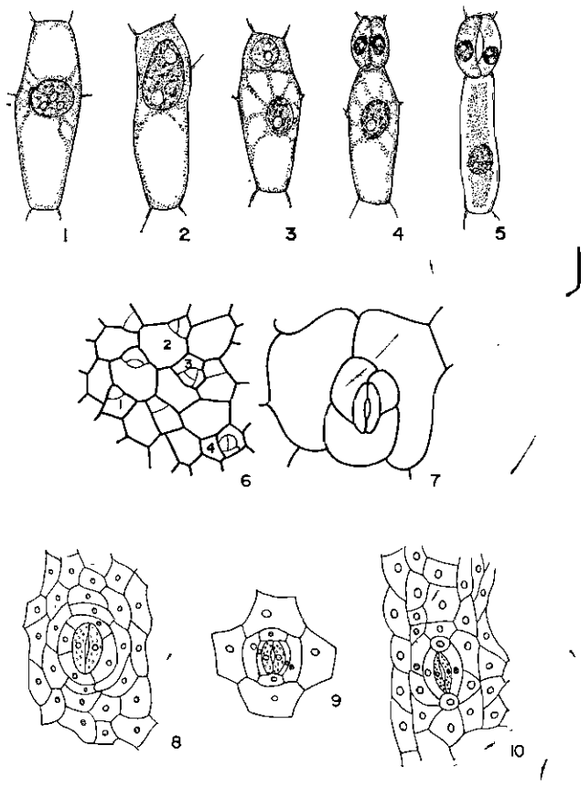

FIG. 62. 1–5, Ontogeny of stomata of *Allium cepa;* 1 and 2, Elongated epidermal cells before unequal division; 3, Showing that the smaller cell resulting from this division is richer in protoplasm. It is this cell that gives rise, by a longitudinal division, to the two guard cells which in no. 4 are not yet separated by the stomatal aperture. In no. 5 the stomatal aperture has developed. 6 and 7, Epidermis of *Sedum pubescens.* 6, Early stages in the development of stomata up to the stage where three subsidiary cells and two guard cells, but no aperture, can be distinguished. Numerals indicate ontogenetic stages. 7, Portion of epidermis with mature stoma. 8–10, Types of monocotyledonous stomata. 8, *Strelitzia nicolei.* 9, *Commelina communis.* 10, *Pandanus haerbachii.* (Nos. 1–5, adapted from Bünning and Biegert, 1953; nos. 8–10, adapted from Stebbins and Khush, 1961.)

laceae and Mimosaceae, some genera of the Papilionaceae, such as *Ononis*, *Arachis*, *Phaseolus* and *Psoralea*, and various species of other families.

4. The *caryophyllaceous* or *diacytic type* (Fig. 61, no. 3) in which each stoma is surrounded by two subsidiary cells, the common wall of which is at right-angles to the longitudinal axis of the stoma. This type is common in the Caryophyllaceae, Acanthaceae and others.

Recently an attempt has been made to classify the stomatal complex of monocotyledonous leaves (Stebbins and Khush, 1961). The following types have been distinguished.

1. That type in which the guard cells are surrounded by four to six subsidiary cells (Fig. 62, no. 8). This type is common in many species of the Araceae, Commelinaceae, Musaceae, Strelitziaceae, Cannaceae and Zingiberaceae.

2. That type in which the guard cells are surrounded by four to six subsidiary cells of which two are roundish, smaller than the rest and are situated at the ends of the guard cells (Fig. 62, no. 10). This type is found in many species of the Palmae, Pandanaceae and Cyclanthaceae.

3. That type in which the guard cells are accompanied laterally by two subsidiary cells—one on each side (Fig. 62, no. 9). This type is found in many species of the Pontederiaceae, Flagellariaceae, Butomales, Alismatales, Potamogetonales, Cyperales, Xyridales, Juncales, Graminales and others.

4. That type in which the guard cells are not associated with any subsidiary cells (Fig. 56, no. 3). This type can be seen in many species of the Liliales (with the exception of the Pontederiaceae), the Dioscoreales, Amaryllidales, Iridales, Orchidales and others.

Ontogeny of stomata

The stomata develop from the protoderm (Fig. 62, nos. 1–7; Fig. 63, nos. 1–6; Fig. 64, nos. 1, 2). The mother cell of the guard cells (Fig. 62, no. 3) is usually the smaller of the two cells that result from an unequal division of a protodermal cell (Bünning and Biegert, 1953; Bonnett, 1961, and others). The mother cell divides to form two cells which differentiate into the guard cells. At first these cells are small and have no special shape but, as they develop, they enlarge and become characteristically shaped. During their development the middle lamella between the two guard cells swells and becomes lens-shaped shortly before the time when it disintegrates to form the stomatal aperture (Ziegenspeck, 1944). Even in those cases in which the mature guard cells are sunken or raised relative to the ordinary cells of the uniseriate epidermis, the guard-cell mother cells and the guard cells are level with the other epidermal cells immediately after their formation. The sinking and the raising is brought about during the maturation

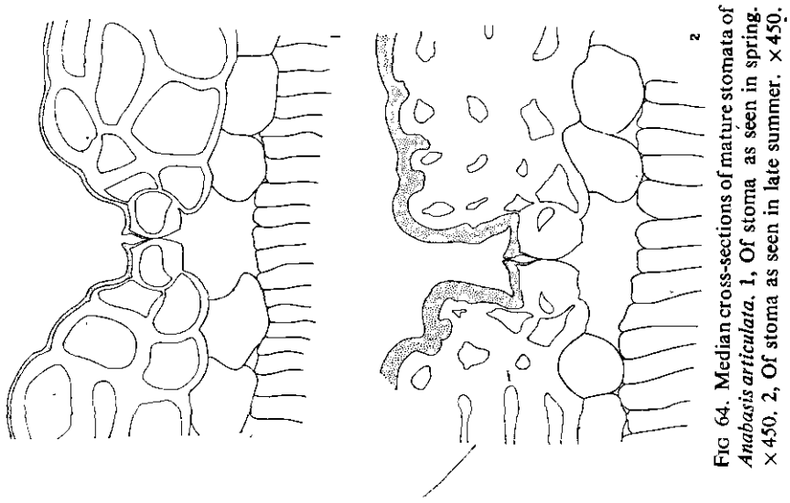

FIG 64. Median cross-sections of mature stomata of *Anabasis articulata*. 1, Of stoma as seen in spring. ×450. 2, Of stoma as seen in late summer. ×450.

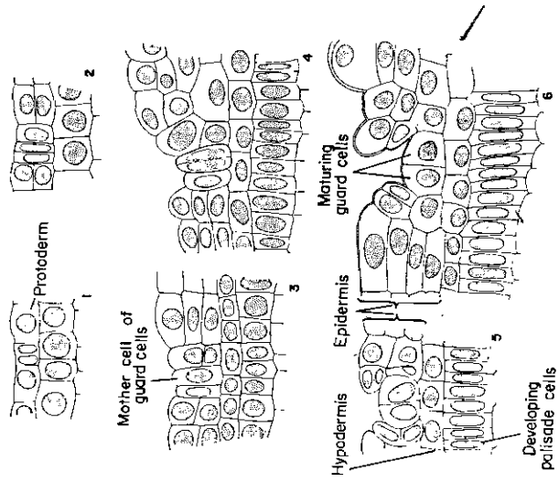

FIG. 63. Ontogeny of the stomata and multiseriate epidermis in *Anabasis articulata*. ×400.

of the guard cells. The development of stomata in the leaf continues for a relatively long period during the growth of the leaf.

On the basis of the order of the appearance of the stomata on the photosynthesizing organ, two main types of development can be distinguished: (1) that in which the stomata appear gradually in a basipetal sequence, i.e. from the tip of the organ to its base, as is the case in leaves with parallel venation and in the internodes of the articulated species of the Chenopodiaceae; (2) that in which there is no regularity in the appearance of the stomata in the various regions of the growing organ, as is the case in leaves with reticulate venation.

EPIDERMAL APPENDAGES

All unicellular and multicellular appendages of the epidermis are designated by the term *trichome*. More massive structures, such as warts and spines (e.g. the thorn of *Rosa*), which consist of epidermal as well as subepidermal tissues, are termed *emergences*. In some cases it is difficult to distinguish clearly between these two types of appendage.

The use of trichomes in taxonomy is well known. Some families can be easily identified by the presence of a particular type or types of hair. In other cases the hairs are important in the classification of genera and species (Metcalfe and Chalk, 1950; Metcalfe, 1963).

Trichomes can be classified into several types (Solereder, 1908; Foster, 1950; Metcalfe and Chalk, 1950; Uphof, 1962).

1. Non-glandular trichomes

(a) Simple unicellular or multicellular uniseriate, non-flattened hairs, as are common, for example, in the Lauraceae, Moraceae, *Triticum*, *Hordeum*, *Pelargonium* and *Gossypium*. In *Gossypium* the fibres used in commerce constitute unicellular epidermal hairs, which may be up to 6 cm long and which are located on the seed coat. This group includes papillae and bladders, which are also known as *vesiculate hairs*. Good examples of the latter can be seen in *Atriplex* (Fig. 65, no. 5) where the vesicle dries out during maturation so that the salt content remains on the leaf surface as a white, powdery layer.

(b) Squamiform hairs which are conspicuously flattened, multicellular hairs. These may be sessile and are then termed scales, or stalked and are then known as peltate hairs. Peltate hairs occur, for example, in *Olea* (Fig. 66, nos. 1, 2).

(c) Branched, multicellular hairs which may be stellate, e.g. in *Styrax* (Fig. 65, nos. 2, 3) or candelabrum-like, e.g. in *Platanus* and *Verbascum* (Fig. 65, no. 1).

(d) Shaggy hairs which consist, at least at the base, of two or more contiguous rows of cells. Such hairs may be seen on the petiole base of *Portulaca oleracea* (Fig. 65, no. 4), in *Schizanthus,* and certain species of the Compositae.

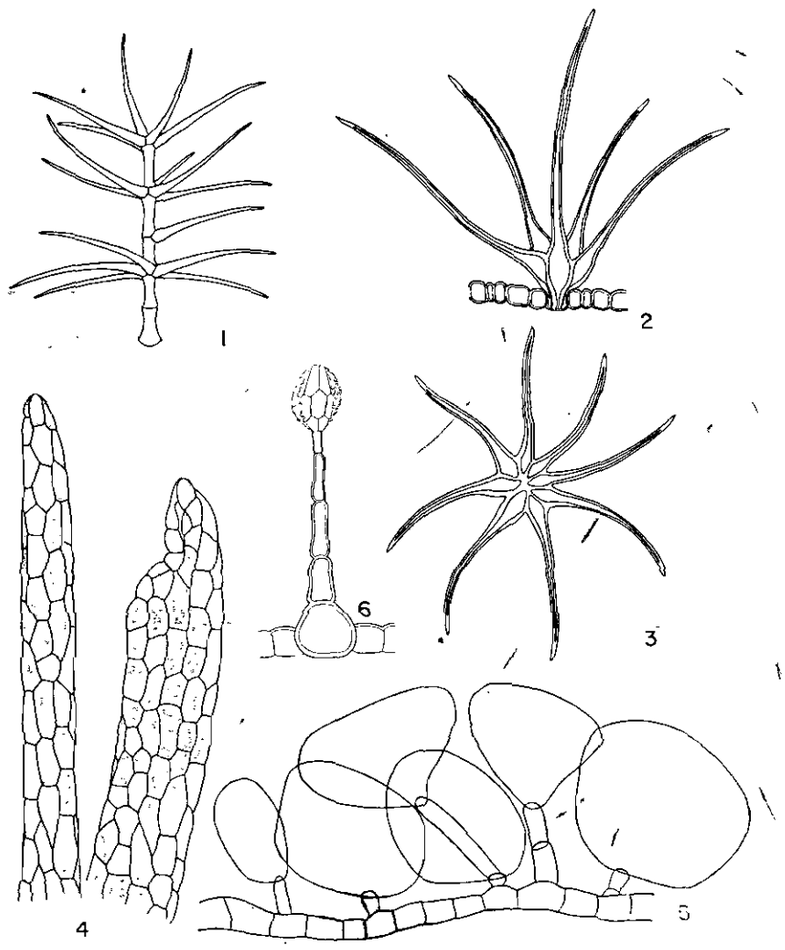

FIG. 65. Different types of trichomes. 1, Candelabrum-like, branched, multicellular trichome from the leaf of *Verbascum.* 2, Stellate multicellular trichome from the leaf of *Styrax officinalis;* lateral view showing how the trichome arises from between ordinary epidermal cells. 3, As in no. 2, but surface view. 4, Shaggy hairs as seen at the base of the petiole of *Portulaca oleracea.* 5, Vesiculate hairs of *Atriplex portulacoides.* 6, Colleter of *Ononis natrix.*

In some species the hairs may show movements. This may be brought about in two ways: either by hygroscopic mechanisms, that is, by the differential swelling and shrinking of the cell walls (e.g. as on the seed of

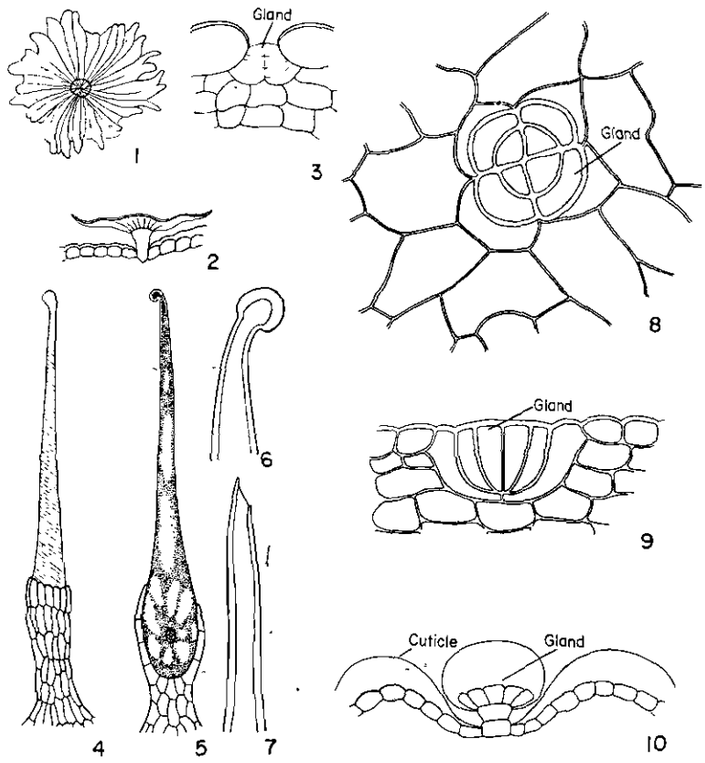

FIG. 66. Trichomes and epidermal glands. 1 and 2, Peltate hair *of Olea europaea.* 1, Surface view showing in the centre the stalk cell around which the "shield" develops. 2, Lateral view. 3, Portion of cross-section of the leaf of *Tamarix* showing a multicellular salt gland. 4–7, Stinging hair of *Urtica dioica.* 4, As seen under a microscope with the focus on the surface of the trichome. 5, As in no. 4, but with focus on centre of the trichome. 6, Intact tip. 7, Trichome with broken tip. 8 and 9, Calcium-secreting gland in epidermis of *Plumbago capensis.* 8, In surface view of the epidermis. 9, In cross-section of the leaf. 10, Portion of a cross-section of the leaf of *Thymus capitatus* showing a secretory gland. (Nos. 4–6, adapted from Troll, 1948.)

Tamarix); or by the action of living cells which may comprise the hair itself or which may be present only at the base of the hair or close to it (Uphof, 1962).

2. Glandular trichomes

These may be unicellular, multicellular or scale-like. The simple multicellular glandular trichomes consist of a stalk and a uni- or multicellular head. Such trichomes occur, for instance, on the leaves of *Nicotiana*, *Primula* and many species of the Labiatae (Fig. 66, no. 10). Certain glandular trichomes consist of a multicellular mass surrounded by palisade-like secretory cells.

Glandular trichomes, which secrete a sticky substance and which usually consist of a multicellular stalk and head, have been termed *colleters*. Such trichomes are mainly found on bud scales and stipules, e.g. of *Rosa*, *Syringa*, *Aesculus* and on the stems and leaves of *Ononis*, and on the calyx of *Plumbago capensis*.

Another type of glandular trichome is the *digestive gland* which is found on insectivorous plants, e.g. in the Nepenthaceae, Droseraceae and Sarraceniaceae.

Highly specialized glandular trichomes are the stinging hairs of *Urtica*. These trichomes consist of a single, long cell which has a broad, bladder-like base and narrow, needle-like upper part (Fig. 66, nos. 4–7). The broad base is surrounded by epidermal cells which are raised above the level of the other epidermal cells. The wall of the distal needle-like part of the secreting cell is impregnated with silica at the tip and with calcium somewhat lower. The very tip is spherical and breaks off, along a predetermined line, when the hair is touched. The broken tip resembles the tip of a syringe and so easily penetrates the skin into which the poisonous, irritating cell contents (hystamine and acetylcholine) are injected.

Uni- and multicellular appendages exist from which nectar is secreted. Some of these are devoid of cuticle and the nectar is secreted by diffusion, while others have a cuticle and then the secreting mechanism is more complex. In the latter the outermost layer of the cell wall of the head of the secreting trichome gradually swells and expands so that a crescent-shaped mucilaginous layer is formed below the cuticle. This layer continues to enlarge and so depresses the innermost layer of the cell wall toward the cell lumen which becomes almost obliterated. Eventually the cuticle bursts and the mucilaginous mass, in which the nectariferous substances have accumulated, is brought to the surface (e.g. *Hibiscus*, *Abutilon* and *Tropaeolum*). Active secretory cells have a dense protoplast. External glandular layers may develop on epidermal outgrowths and emergences, or independently of them. Thus, for instance, nectariferous tissues may occur on the teeth of leaf margins (*Prunus amygdalus*, *Ailanthus altissima*) or on different parts of the floral organs. The manner of secretion from these glands differs in the various plant species. Here also the secretion may be accomplished by simple diffusion, by the swelling of the outermost layers of the epidermal cell wall and the rupture of the cuticle, or special aper-

tures, which are modified stomata, may be present on the epidermis (Fahn, 1952). (See Chapter 19 for further details.)

Multicellular epidermal glands of special interest are the *salt* and *chalk glands*. These glands are somewhat sunken or are level in relation to the epidermis. Salt-secreting glands (Fig. 66, no. 3; Fig. 67, nos. 1, 2) are

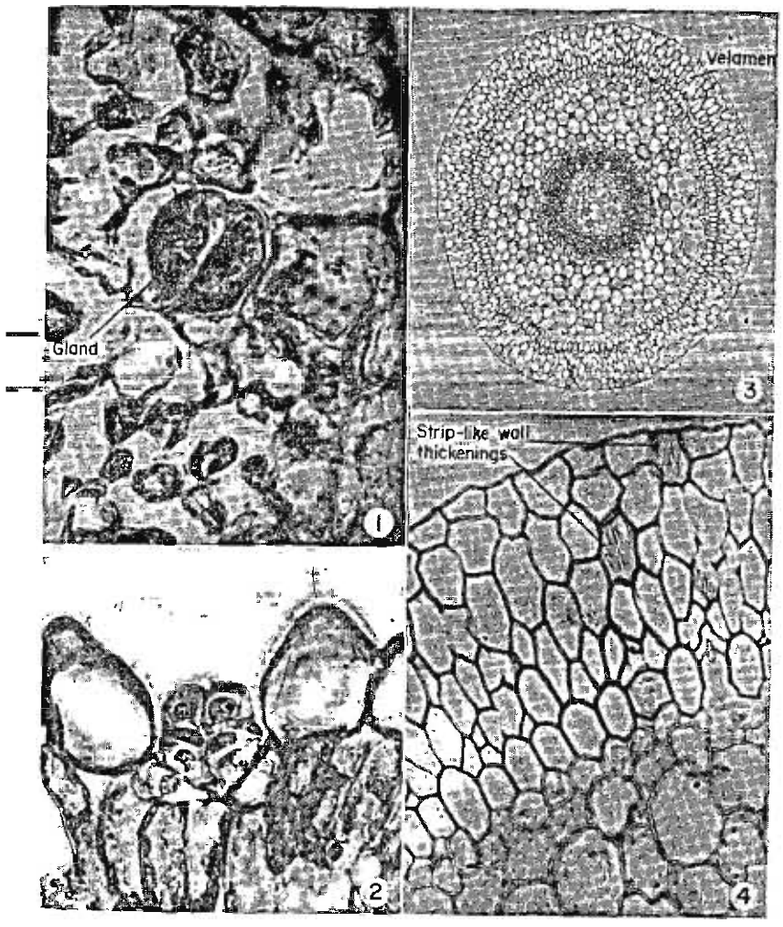

FIG. 67. 1 and 2, Salt-secreting gland on the leaf of *Tamarix*. 1, In tangential section. ×520. 2, In cross-section. ×600. 3, Cross-section of the aerial root of an epiphytic orchid, in which it is possible to distinguish the velamen. ×35. 4, As in no. 3, but outer portion, consisting mainly of velamen, enlarged. ×200; in some of the cells the walls, with strip-like thickenings, which strengthen the cells, can be seen.

common in the Tamaricaceae (Volkens, 1887; Brunner, 1909). These glands secrete other salts in addition to sodium chloride. Chalk glands are common in the Plumbaginaceae (Fig. 66, nos. 8, 9) where they sometimes secrete mucilage in addition to calcium carbonate (Metcalfe and Chalk, 1950).

Multicellular trichomes develop from a single initial which is situated among the other epidermal cells. This cell elongates and then undergoes a number of divisions. The cells of multicellular trichomes may develop secondary walls, and in some cases the walls even become lignified.

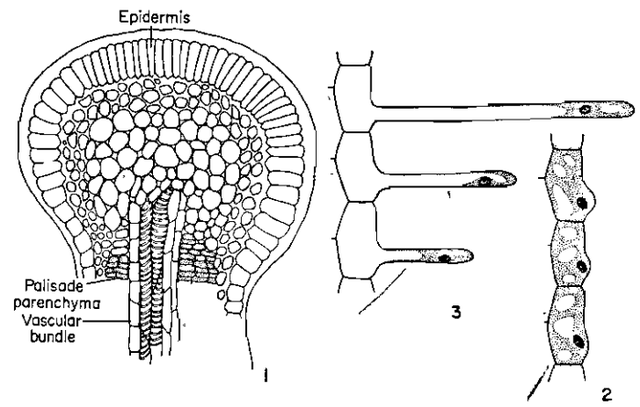

FIG. 68. 1, Longitudinal section through a gland present on the petiole of *Prunus amygdalus* showing a palisade-like secretory epidermis. 2 and 3, Development of root hairs. 2, Epidermal cells showing the beginning of a protuberance at the apical end of the cell. 3, Maturing root hairs that develop from the above protuberances as the cells become further distant from the root apex. (Nos. 2 and 3, adapted from Troll, 1948.)

Root hairs are tubular elongations of epidermal cells. They are branched in only very few plants. Root hairs are 80–1500 μ long and 5–17 μ in diameter (Dittmer, 1949). The root hairs have large vacuoles and they are usually thin-walled. On the aerial, adventitious roots of *Kalanchoë fedtschenkoi* multicellular root hairs have been found (Popham and Henry, 1955).

Root hairs begin to form beyond the meristematic zone of the young roots in regions where the epidermal cells can still elongate. The root hairs usually first appear as small protuberances near the apical end of the epidermal cell. If the epidermal cell continues to elongate after the appearance of the protuberance the root hair is found somewhat distant from the apical end of the mature epidermal cell (Fig. 68, nos. 2, 3). Root hairs

elongate at their tips where the wall is thinner, softer and more delicate. The nucleus is usually located close to the growing tip of the root hair. The epidermal cells which give rise to root hairs elongate less than the other epidermal cells. (See Cormack, 1949, for further anatomical and physiological details.)

In some plants only certain of the root epidermal cells, termed *trichoblasts* or *piliferous cells*, can produce root hairs. These are small cells which result from unequal divisions of epidermal cells.

Root hairs are usually viable for only a short period, generally only a few days. With the death of the root hairs and if the cells are not sloughed, the walls of the epidermal cells become suberized and lignified. In some plants root hairs have been found that remain permanently on the plant. The walls of such root hairs become thick and then apparently lose their ability to take up water from the soil (Artschwager, 1925; Cormack, 1949).

Both ontogenetically and functionally the epidermis may be considered as a separate tissue. The epidermis develops from the protoderm by continuous anticlinal cell divisions. As it is a compact tissue, devoid of intercellular spaces and covered with a cuticle, the epidermis provides protection to all those plant organs that consist entirely, or almost so, of primary tissues.

The specialized cells of the epidermis are of great interest as they usually are of characteristic structure, ontogenetic development and function. They are also of great value in the study of taxonomic and evolutionary problems. Specialized cells, such as the trichoblasts and guard cells, are the products of unequal cell divisions and they arise from the smaller of the two cells thus formed. Bünning (1952, 1953) has already drawn attention to this phenomenon which is characteristic not only for the epidermis but also for idioblasts, such as raphide-containing cells and idioblastic sclereids, which develop in inner tissues. Bünning states that the small embryonic cells, which are capable of varied development, are at first qualitatively equal and that their consequent development is, therefore, controlled by factors which as yet have not been analysed.

Till now no satisfactory explanation has been given of the phylogeny and functional significance of certain of the specialized cells, such as the bulliform, silica- and cork-cells of grass leaves.

Several types of arrangement of the subsidiary cells around the guard cells are recognized in both monocotyledons and dicotyledons. In relation to the dicotyledons, no conclusions have been put forward as to the evolutionary trends among these types. For the monocotyledons, Stebbins and Khush (1961) suggest that the type with four or more subsidiary cells is the most primitive, and that those types with few subsidiary cells or those lacking them entirely have been derived, independently, from this primi-

tive type by reduction. It should be mentioned, however, that this evolutionary trend does not correlate with that of other anatomical characteristics, such as the evolution of the tracheary elements, for instance. It is seen, therefore, that additional research should be made in this field.

As regards the opening and closing of the stomatal aperture, the structure of only a few types of guard cell has been thoroughly investigated. There are indications that the variations in guard-cell structure result in different opening and closing mechanisms. In certain cases, such as in hydathodes and nectaries, the stomata are so modified that their apertures remain open permanently.

In some desert plants the walls of the guard cells become cutinized and thickened at the end of the summer to such an extent that the cell lumen is almost completely obliterated. Therefore it was suggested (Volkens, 1887) that stomata with such guard cells remain closed during the critical drought period. This is a feature of extreme interest and further study may lead to a better understanding of the anatomical adaptations of desert plants.

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PRIMARY VEGETATIVE BODY OF THE PLANT

IN THE previous chapters the structure of the tissues, the type of cells of which they consist and the structure and characteristics of these cells, have been considered. In the present chapter the arrangement of and interrelationship between these tissues in the different vegetative organs of the primary body of the sporophyte will be discussed. An attempt will also be made to explain the structure of the primary body both from a functional and from a phylogenetic standpoint.

The vegetative organs that will be discussed next are the *stem*, the *leaf* and the *root*. It is difficult, however, to distinguish between the stem and the leaves—these organs develop from a common meristem, i.e. from the apical meristem of the shoot apex. The connection between and mutual dependence of these two organs exist throughout the entire growth period of the plant (Wetmore, 1943; Wardlaw, 1960). Arber (1950) claims that the leaf is actually a stem-like structure which has secondarily become flattened. In certain ferns leaf primordia were diverted from producing leaves and were induced to become buds when wide and deep incisions were made around them in the shoot apex (Cutter, 1959). Thus the stem and leaf are regarded as a complex unit and are given the common term *shoot*.

The acceptance of this relationship and connection between the stem and the leaf enables a more thorough understanding of the primary structure of the stem.

CHAPTER 11

THE STEM

Ontogenetic development of the stem

The axis of the embryo in the seed consists of a *hypocotyl* and *radicle*. At the tip of the hypocotyl one or more cotyledons and the bud of the shoot, i.e. the *plumule*, are found. At the tip of the radicle is the root cap.

The bud of the shoot usually consists of an axis containing a few internodes, which have not elongated, and some leaf primordia. With the

germination of the seed the embryo enlarges and starts to grow, the apical meristem of the young shoot adds further leaf primordia and the internodes between the lower primordia, which in the meantime have become distant from the apex, elongate. In many plants buds develop in the axils of the developing leaves giving rise to a branched shoot.

In mature plants the development of leaf primordia at the shoot apex and the elongation of the nodes below it are the same as that in the growing embryo of the germinating seed. The order of appearance and the arrangement of leaves on the stem is more or less characteristic of each species.

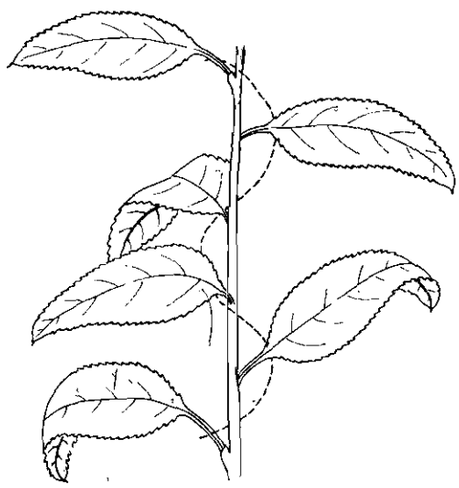

FIG. 69. Portion of a branch of *Prunus*. The broken line which passes from leaf to leaf indicates the phyllotaxis which, in this case, is $\frac{2}{5}$.

That part of the stem from which a leaf or leaves develop is called the *node* and that portion of the stem between two such nodes, the *internode*. The length of the internodes varies in the different species. In certain plants, such as *Cichorium*, *Thrincia* and others, where the leaves are arranged in a basal rosette, the internodes hardly elongate at all, but in most spermatophytes the internodes elongate to differing extents. At each node one, two or more leaves may be found. The arrangement of the leaves on the stem is termed *phyllotaxy*. When there are more than two leaves at one node the arrangement is termed *whorled*. When there are two leaves at each node the leaves are said to be *opposite*; in this type of arrangement the leaves of the successive nodes may be at right-angles to each other and then the arrangement is termed *decussate*; or the leaves may form two parallel ranks along the stem, i.e. *distichous*. When there is a single leaf at each node and the leaves are arranged spirally on the stem the phyllotaxy is said to be

alternate. The space, on the circumference of the stem, between two successive leaves, whether they arise at a single node or whether they are arranged spirally on the stem, is constant, i.e. two successive leaves are separated by a constant portion of the perimeter of the stem (Fig. 69).

The position of the leaf primordia on the stem apex is determined before it is possible to distinguish any feature that indicates that such development has begun. Therefore it appears that the factors determining the position of the primordia on the stem apex are internal and, in general, they are identical with those factors that control the distribution of the growth potential in the apical meristem. There is reason to assume that each leaf, together with that portion of the axis around it and below its junction to the axis, forms a single physiological unit. Such *leaf fields* or *primordial fields* are already present in the shoot apex. This association between stem and leaf is evident, among others, in the relationship between the phyllotaxy and the vascularization and general structure of the stem.

Arrangement of primary tissues in the stem

The primary body develops from the protoderm, procambium and ground meristem. The arrangement and structure of the primary tissues is as follows.

THE EPIDERMIS

Externally, the stem is bounded by the epidermis which contains, apart from the typical epidermal cells, guard cells, idioblasts and different types of trichomes (see Chapter 10).

THE STEM CORTEX

The stem cortex is that cylindrical region between the epidermis and the vascular cylinder (Fig. 70, nos. 1–4; Fig. 82, no. 2). It may comprise various cell types. In the simplest case, the cortex consists entirely of thin-walled parenchyma tissue. In many stems, as for instance *Pelargonium*, *Retama* and *Salicornia*, this parenchyma may have a photosynthetic function in addition to that of the temporary storage of starch and other metabolites. In other cases the outer region of the cortex, which borders on the epidermis, may include collenchyma or fibres, and the inner region of parenchyma. The collenchyma or fibres may form a continuous cylinder or they may be present in the form of separated strips. The stem cortex may contain sclereids, secretory cells and laticifers.

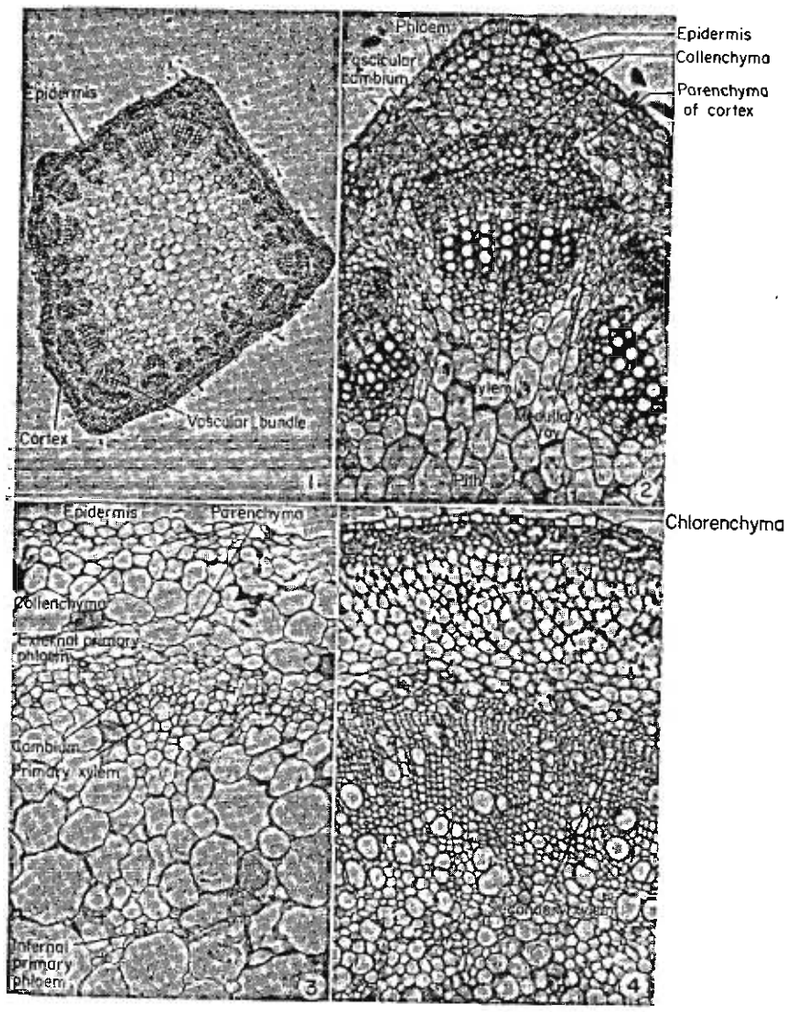

FIG. 70. 1, Cross-section of a young stem of *Medicago sativa*. ×30. 2, Portion of 1, enlarged. ×115. 3 and 4, Portions of cross-sections of a stem of *Lycopersicon esculentum*. 3, A young stem in which internal phloem can be distinguished. ×85. 4, A mature stem in which it is possible to distinguish that the cortical parenchyma below the epidermis has developed into chlorenchyma and that a fair amount of secondary xylem has been produced. ×95.

THE ENDODERMIS

In the stem difficulty exists in determining the anatomical border between the cortex and the stele (Esau, 1950) as in stems a distinct *endodermis*, i.e. a layer of specialized cells which delimits the cortex from the vascular cylinder, is not usually developed. It has not yet been clarified if the endodermis is ontogenetically related to the cortex or to the stele.

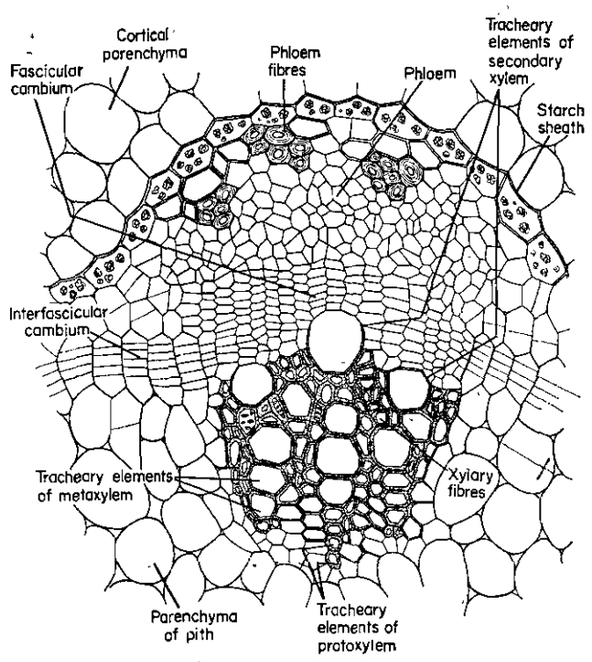

FIG. 71. Portion of a cross-section of a well developed hypocotyl of *Ricinus*. (Adapted from Palladin, 1914.)

Morphologically, a well developed endodermis is a compact layer of living cells which form a hollow cylinder. The walls of the endodermal cells are of characteristic and specialized structure. In the typical cells, bands and strips which contain lignin and suberin, apart from cellulose, are present on the radial and transverse walls; these are called *Casparian strips* or *Casparian bands* (Fig. 111, nos. 2, 3). In the course of maturation the endodermal cells may undergo changes that involve the addition of suberin lamellae on the entire inner surface of the cell walls. This may be followed by the addition of a secondary layer of cellulose, which may sometimes contain lignin, on the inside of suberin lamellae. (See also Chapter 13.)

The endodermis is most conspicuous in the stems of the lower vascular plants. Here the cell walls have Casparian strips and a suberin lamella, and the endodermis surrounds the vascular tissue. It is sometimes also found between the vascular cylinder and the pith (*Marsilea*, *Ophioglossum* and others). In certain ferns, e.g. *Dryopteris*, the endodermis surrounds the individual bundles. In the spermatophytes the endodermis is usually most obvious in the root, but, in some herbaceous plants, Casparian strips can also be observed in the endodermis of the stem. In stems, however, a typical endodermis is more usually found in underground stems, such as rhizomes, than in aerial stems. In the herbaceous stems of *Senecio* and *Leonurus* the endodermis is developed only when the plant reaches the flowering stage.

The innermost cortical layer of young dicotyledonous stems usually contains many large starch grains (Fig. 71). This layer has been termed the *starch sheath*, and, because of its position, it is considered to be homologous with the endodermis.

Different investigations have shown that, in some monocotyledons, an endodermis with typical secondary cell walls may be caused to develop to a greater extent under the influence of external factors, such as the lack of nitrogenous salts and a high degree of aeration of the soil, among others (Van Fleet, 1942a, b; 1950a, b). In some dicotyledonous stems Casparian strips may develop under conditions that cause etiolation (Priestley, 1926).

In the stems of the lower vascular plants and in the roots of all vascular plants, the pericycle can readily be located between the endodermis and the vascular tissues. The existence of the pericycle as a separate tissue in the stems of spermatophytes is questionable. The tendency is to relate ontogenetically any tissue between the cortex and the phloem to the phloem (Blyth, 1958).

THE PRIMARY VASCULAR SYSTEM

Internal to the cortex is the vascular system of the stem. In the gymnosperms and most of the dicotyledons the vascular system consists of a continuous or a split cylinder which encloses the *pith*, i.e. the central portion of the stem (Fig. 70, no. 1; Fig. 77, nos. 1–4). In this cylinder two types of vascular tissues can be distinguished—the phloem which is usually external, and the xylem which is usually internal. In the case of the split cylinder each strand is termed a *vascular bundle*. A vascular bundle in which the phloem is only external to the xylem is said to be a *collateral bundle* (Fig. 70, no. 2; Fig. 72, nos. 3, 4; Fig. 83, no. 1). In some dicotyledonous families, e.g. the Solanaceae, Cucurbitaceae, Asclepiadaceae, Apocynaceae, Convolvulaceae and Compositae, internal phloem is also present. The internal phloem may be present as separate strands on the border of the pith,

as in *Lycopersicon* (Fig. 70, no. 3), or it may be in close contact with the inner side of the xylem, as in the stems of the Cucurbitaceae and Myrtaceae. The latter type of bundle is termed a *bicollateral bundle* (Fig. 82, no.

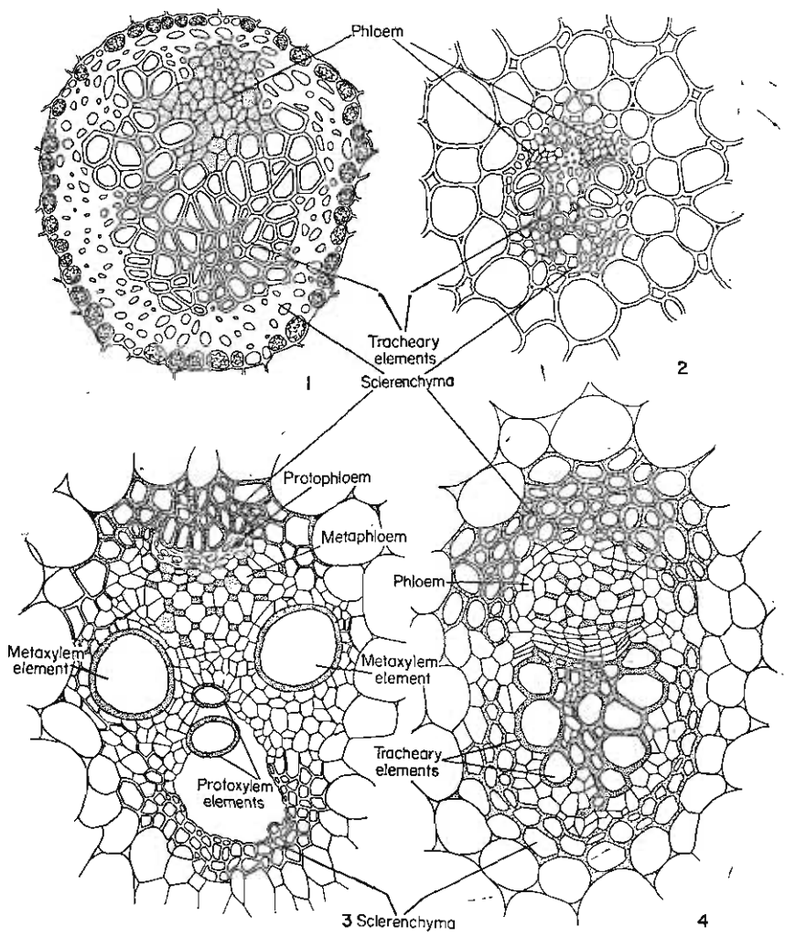

FIG. 72. Cross-sections through vascular bundles of different types. 1, Stem bundle of *Kingia*. 2, Foliar bundle of *Xanthorrhoea*. 3, Stem bundle of *Zea*. 4, Stem bundle of *Ranunculus*. (Nos. 3 and 4, adapted from Palladin, 1914.)

2). In some monocotyledons, as for example *Convallaria majalis*, *Acorus*, some genera of the Xanthorrhoeaceae, as well as the secondary bundles of *Aloë arborescens*, *Dracaena*, *Cordyline* and others, the xylem surrounds

the phloem. Such bundles are termed *amphivasal bundles* (Fig. 83, no. 3). Bundles common in the Pteridophyta, in which the phloem surrounds the xylem are termed *amphicribral bundles*. There are also bundles in which the xylem is seen to be V- or U-shaped in cross-section. In the former, as can be seen in the leaf of *Xanthorrhoea*, for example, the phloem groups are situated at the free ends of the xylem arms (Fig. 72, no. 2). In the case of U-shaped xylem the phloem is surrounded on three sides by xylem; such bundles occur in the stem of *Asparagus aphyllus* and *Kingia australis* (Fig. 72, no. 1).

In most monocotyledons and in a few dicotyledons no distinct vascular cylinder exists, and the primary vascular system consists of a large number of bundles which are scattered irregularly, and it is impossible to distinguish clearly the boundary between the cortex, the vascular cylinder and the pith (Fig. 82, no. 1).

The vascular system plays an important role in the attempt to solve phylogenetic problems. The vascular system has been thoroughly investigated, by comparative methods, both from plants living today and from fossil forms. Van Tieghem and Douliot (1886) proposed the *stelar theory* to explain the structure of the plant axis. This theory greatly influenced later investigators who worked on the comparative anatomy of the Tracheophyta. According to the above theory the gross anatomical structure of the root and stem is similar, i.e. in both of them the cortex surrounds a central core which they termed the *stele*. The stele comprises the *pericycle*, i.e. the non-vascular tissue between the phloem and cortex, the *vascular tissues* and the *pith*, when present.

Medullary and cortical bundles, present on the inside and outside of the stele respectively, are found in certain plants (De Bary, 1877; Eames and MacDaniels, 1947; Metcalfe and Chalk, 1950). These bundles are associated with stems of both anomalous and typical structure. Medullary bundles occur in numerous dicotyledonous families, e.g. in the Amaranthaceae, Chenopodiaceae, Orobanchaceae, Berberidaceae and Cucurbitaceae. Cortical bundles are less common and are known to occur, for example, in the Melastomaceae, Proteaceae, Araliaceae and Calycanthaceae. So-called "cortical" bundles are often leaf-traces which descend through the cortex for some distance before entering the stele, e.g. as in *Begonia* and *Casuarina*. In many plants, with reduced leaves and a fleshy, photosynthetic cortex, branches from the base of the leaf-trace penetrate into the cortex (Eames and MacDaniels, 1947; Fahn, 1963).

TYPES OF STELE

According to Smith (1955), Esau (1953) and other authors, the stele of the sporophyte of vascular plants may be divided into two basic types: (1) *protostele* which consists of a solid central cylinder of xylem surrounded

by phloem; and (2) *siphonostele* in which there is a cylinder of pith within the xylem. Both ontogenetically and phylogenetically the protostele is the more primitive, and it is thought that the siphonostele has developed phylogenetically from the protostele.

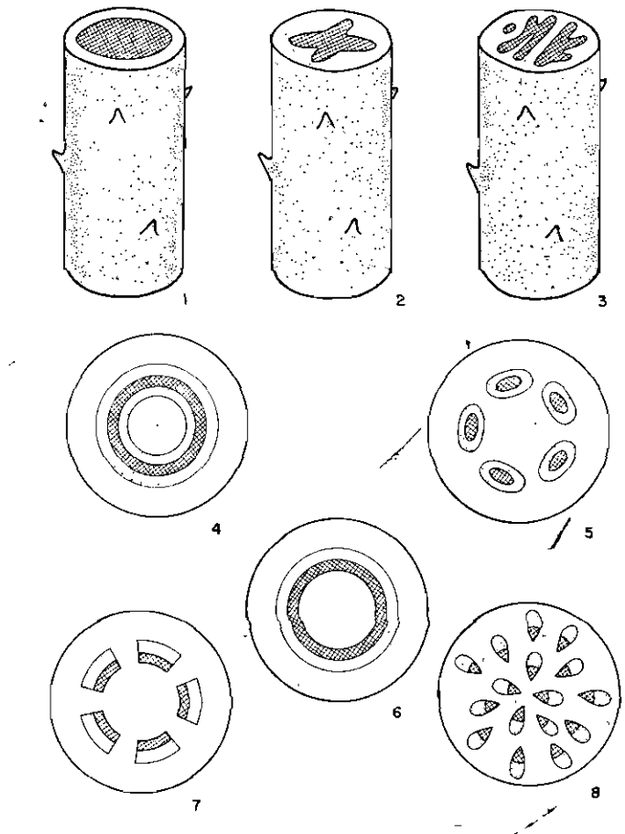

FIG. 73. 1–3, Three-dimensional diagrams of different types of protostele. The diagrams represent the stele alone without the cortex and epidermis. The microphylls appear in those positions where there are protuberances on the surface of the stele. 1, Haplostele. 2, Actinostele. 3, Plectostele. 4–8, Diagrams of cross-sections of stems with siphonosteles showing different stages in evolutionary development. 4, Amphiphloic siphonostele (solenostele). 5, Dictyostele. 6, Ectophloic siphonostele. 7, Eustele. 8, Atactostele. Xylem—hatched; phloem—stippled.

Three types of protostele can be distinguished: (1) *haplostele* (Fig. 73, no. 1) which is the simplest type, in which the xylem appears more or less circular in cross-section, e.g. *Rhynia* and *Selaginella;* (2) *actinostele* (Fig.

73, no. 2) in which the xylem is stellate in cross-section, e.g. *Psilotum;* and (3) *plectostele* (Fig. 73, no. 3) in which the xylem is split into longitudinal plates of which some are joined and others separate, e.g. *Lycopodium.*

The various types of protostele are characteristic of the Lycopsida (the lower Pteridophyta) and the siphonostele of the Pteropsida (the phylogenetically more advanced Pteridophyta and the Spermatophyta).

Two types of siphonostele are distinguished according to the positions of the phloem and xylem: (1) *ectophloic siphonostele* in which phloem only surrounds the xylem externally (Fig. 73, no. 6); and (2) *amphiphloic*

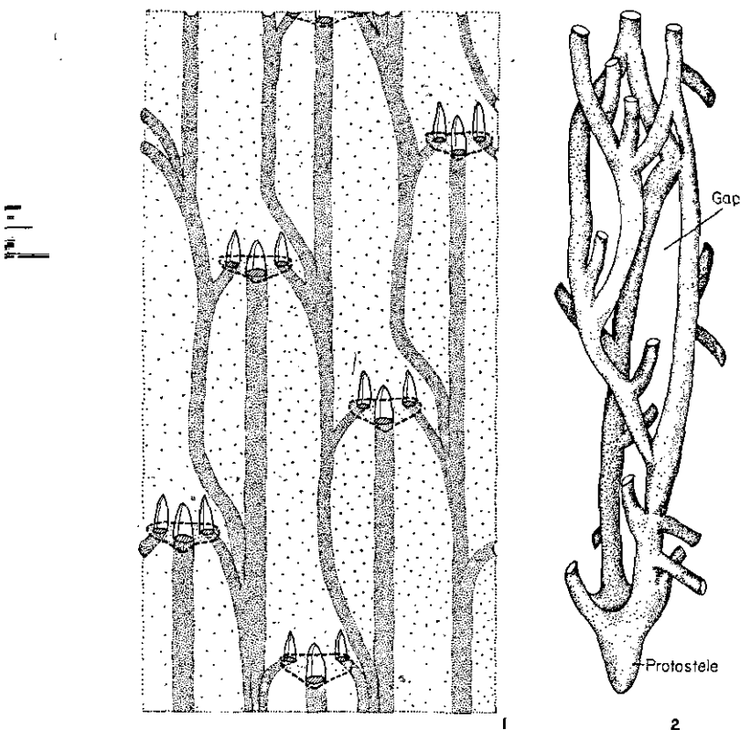

FIG. 74. 1, Diagrammatic representation, on a single plane, of the primary vascular system of *Populus canadensis*; the leaf-gaps are the only interruptions. Heavily stippled areas—protoxylem; lightly stippled areas—metaxylem; unstippled areas—leaf-gaps. The broken line indicates the position of leaf attachment. 2, Three-dimensional diagram of the stele of the rhizome of *Ophioglossum lusitanicum.* The larger part of the stele is dictyostelic and only the small basal portion is protostelic. Both leaf traces (directed upwards) and bundles that enter the roots (directed downwards) arise from the bundles which surround the gaps. (No. 1, adapted from Eames and MacDaniels, 1947.)

siphonostele (Fig. 73, no. 4) in which the phloem surrounds the xylem both externally and internally and where the endodermis appears both outside and inside the vascular tissue on the borders of the cortex and pith, respectively (e.g. *Adiantum* and *Marsilea*).

The siphonostele may consist of a continuous cylinder of vascular tissue or of a network of bundles (Fig. 74, no. 2; Fig. 75, nos. 1–5). The latter type is the more advanced and the vascular tissues of this type appear in cross-

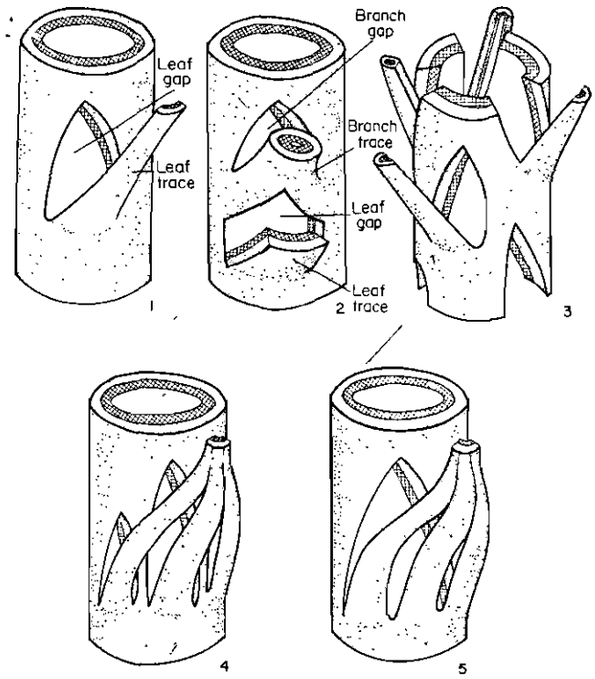

FIG. 75. Diagrams of siphonosteles with different types of arrangement of the leaf- and branch-traces and gaps. 1, Unilacunar node with one leaf-trace. 2, Unilacunar node with associated branch-traces and gap. 3, Overlapping gaps so that the stele forms a network of bundles. 4, Trilacunar node with three leaf-traces. 5, Unilacunar node with three traces.

section as a ring of separate bundles. The regions between the bundles are parenchymatous. Those parenchymatous regions that occur in the stele, above the positions where the leaf-traces pass out from the stele to the leaves, are termed *leaf-gaps* (Fig. 75, no. 1). An amphiphloic siphonostele in which the successive leaf-gaps are considerably distant, one from the other, is termed a *solenostele*. An amphiphloic siphonostele with overlap-

ping gaps, i.e. that in which the lower part of one gap is parallel with the upper part of another gap, is termed a *dictyostele* (Fig. 73, no. 5). In this case the bundles are interconnected to form a cylindrical network (Fig. 74, no. 2) and each bundle is of concentric structure consisting of a central strand of xylem surrounded by phloem. Individually such bundles are termed *meristeles*. From the anatomical point of view these are amphicribral bundles.

During the course of evolutionary development the *eustele* (Fig. 73, no. 7), with collateral bundles, was formed by the splitting of the ectophloic siphonostele. Bicollateral vascular bundles in which the xylem strands are accompanied externally and internally by phloem strands and which are found in advanced dicotyledonous families appear to be the result of a secondary specialization and not a relic of the primitive structure characteristic of the Filicinae.

In some plants, e.g. *Marattia*, *Pteridium* and *Matonia*, two or more concentric cylinders of vascular tissue are present. Such a stele is termed a *polycyclic stele*. The individual cylinders in this case are interconnected. In rare cases stems and roots contain more than one stele; such a condition is termed *polystelic* (see Chapter 13).

A different interpretation of the above nomenclature exists and has been summarized by Sporne (1962). According to this interpretation the ectophloic siphonostele without leaf-gaps, such as is found in the Pteridophyta, is considered as a protostele and is termed a *medullated protostele*. Sporne does not use the term siphonostele for the Pteridophyta.

As in the dictyostele, the bundles of the eustele are usually interconnected. That type of stele in which the bundles are scattered (Fig. 73, no. 8), such as is characteristic of the monocotyledons, is called an *atactostele* (Nast, 1944; Esau, 1953).

In the siphonostele not all the interruptions in the vascular tissue are leaf-gaps as described above. Some interruptions result from the secondary reduction of vascular tissue and the formation of interfascicular parenchyma. Such interruptions are termed *perforations*. When such perforations occur in a solenostele it may be confused with a dictyostele. The parenchymatous connections between the pith and cortex are termed *medullary rays*.

There are certain plants, such as *Populus*, for example (Fig. 74, no. 1), in which the primary vascular cylinder consists of a thin layer of vascular tissue which is interrupted only by leaf- and small branch-gaps. Rib-like projections composed entirely of protoxylem are found on the inner surface of this cylinder (Eames and MacDaniels, 1947).

Differing from the Pteropsida whose steles form leaf-gaps, the steles in microphyllous plants, i.e. the Psilopsida, Lycopsida and Sphenopsida, are devoid of such parenchymatous regions (Fig. 73, nos. 1–3). In microphyllous plants with a siphonostele the only gaps present are *branch-gaps* which

are those gaps associated with bundles that depart from the central cylinder to the lateral branches. This type of siphonostele has been termed by some authors *cladosiphonic*, and that found in the Pteropsida *phyllosiphonic* (Jeffrey, 1910).

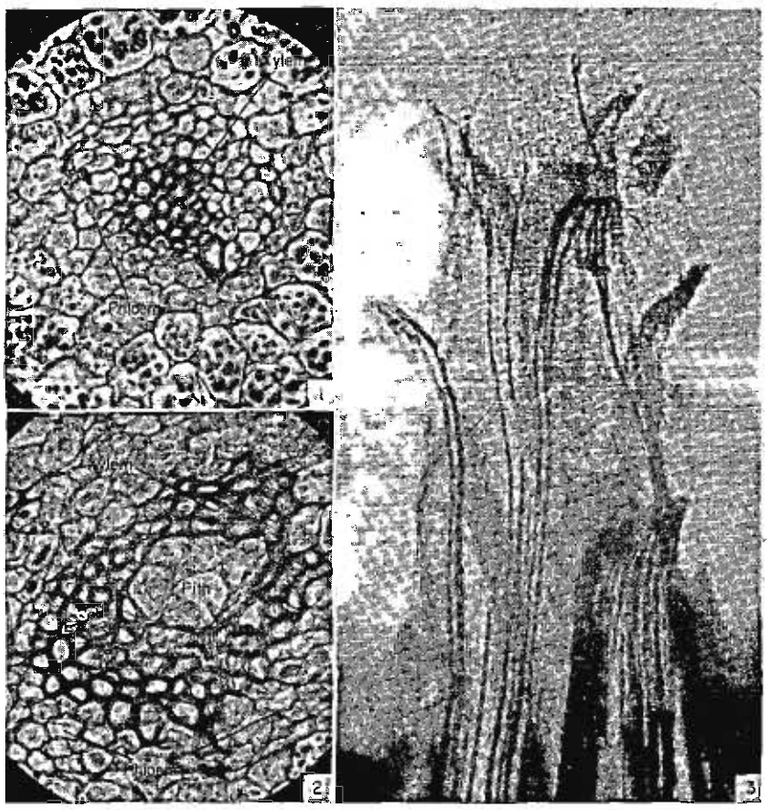

FIG. 76. 1 and 2, Micrographs of the central portion of cross-sections of the erect rhizome of *Ophioglossum lusitanicum* showing the transition from protostele to siphonostele. 1, Protostele. 2, Siphonostele. 3, A branch tip of *Chimonanthus* (a woody genus of the Ranales) cleared by treatment with lactic acid to show the pattern of vascularization in which the nodes are unilacunar with two traces; the traces fuse on entry into the leaf. Nos. 1 and 2, ×200.

The development of siphonostele from the protostele has been a point of discussion (Bower, 1911a, b). According to one view the pith, i.e. the parenchymatous core, in the siphonostele originated from the cortex. The supporters of this view use the presence of the endodermis, in certain

ferns, between the pith and vascular tissue as proof of this view. According to them the endodermis penetrated inwards together with the parenchyma of the cortex, and they explain the absence of such an endodermis in other plants as being the result of further development. According to another theory the siphonostele developed from the protostele by the alteration of the inner vascular initials to parenchyma initials. This theory is supported by the fact that tracheary elements may be found in the centre of the stele scattered among the parenchyma cells. This feature is common in relatively primitive plants, both living and fossil. Such steles may be considered as intermediate stages between protosteles and siphonosteles. In the light of our present knowledge of morphogenesis it is difficult to accept the former theory. Research on *Ophioglossum lusitanicum* (Gewirtz and Fahn, 1960) showed that the stele of the rhizome of the sporophyte that developed from the gametophyte (not as a result of vegetative reproduction) was protostelic at the base and siphonostelic (dictyostelic) in its upper portion. Furthermore, it was clearly seen in the transition zone, below the level of the first leaf-gap, that the pith undoubtedly originated from the xylem. Here parenchyma cells were seen mingled with tracheids and the number of parenchyma cells was seen to increase in an upwards direction (Fig. 76, nos. 1, 2).

ANATOMY OF THE NODE

In the angiosperms, and especially in the dicotyledons, the primary vascular cylinder is interrupted at each node by the exit of one or more bundles that enter the leaves. The stelar bundles, which are the continuation of the bundles in the leaf bases, are called *leaf-traces*. According to the number of leaf-gaps per leaf the node is termed *unilacunar*, *trilacunar* or *multilacunar* (Fig. 75, nos. 1–5; Fig. 77, nos. 1–5; Fig. 74). The anatomy of the node is an important aspect of taxonomy and of the comparative morphology of the stem, leaf and flower. Sinnott (1914) concluded that the trilacunar node is the primitive type in the angiosperms and that the unilacunar node developed, phylogenetically, from it by the loss of the two lateral gaps together with their respective traces, or by the approximation of the lateral traces to the median bundle to form a bundle composed of three traces, which is associated, therefore, with a single gap. Contrary to the reduction in the process of the formation of the unilacunar node, Sinnott states that the multilacunar node is formed by the addition of new gaps and traces.

The assumption that the trilacunar node is the primitive one among the angiosperms has been refuted by recent research on nodal anatomy in the gymnosperms and angiosperms (Gunckel and Wetmore, 1946a, b; Marsden and Bailey, 1955; Marsden and Steeves, 1955; Bailey, 1956; Fahn and

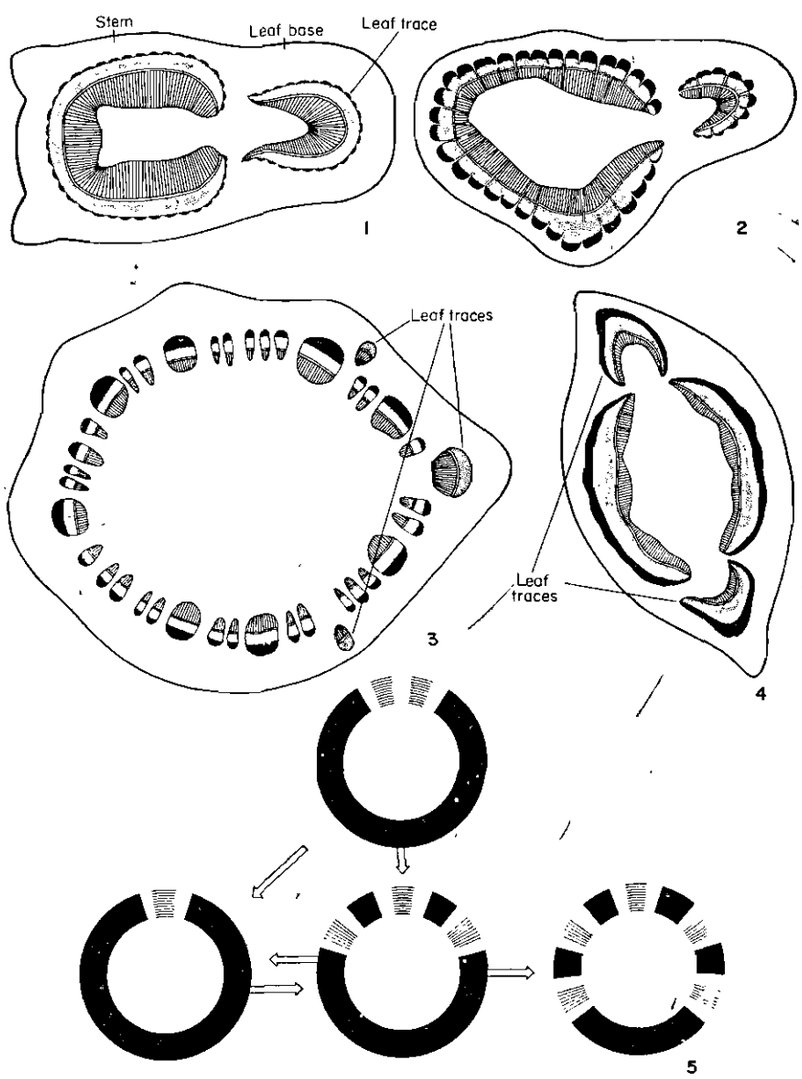

FIG. 77. Diagrams showing the relationship between the vascular systems of the leaf and the stem. 1–4, Cross-sections of the nodes of young stems. 1, *Eucalyptus camaldulensis* in which the node is unilacunar. 2, *Laurus nobilis*, also with unilacunar node. 3, *Chrysanthemum anethifolium* in which the node is trilacunar with three traces. 4, *Dianthus caryophyllus* which has opposite leaves and unilacunar nodes. 5, Diagrams showing the possible ways of development of the nodal vascularization in dicotyledons from the unilacunar node with two traces. (No. 5, adapted from Marsden and Bailey, 1955.)

Bailey, 1957). By these workers and others it has been shown that in many Pteridophyta, in the Cordaitales, Bennettitales, in *Ginkgo* and *Ephedra*, a single gap is found in that position where the leaf-traces depart from the stele. Similarly, in many dicotyledons unilacunar nodes with two leaf-traces have also been found. Many of the dicotyledonous genera with unilacunar nodes with a double leaf-trace belong to the primitive groups of the Ranales and the Chenopodiaceae. Bailey (1956) found in many dicotyledons that the vascular supply to the cotyledons consists of a double leaf-trace which arises from a unilacunar node (Fig. 78).

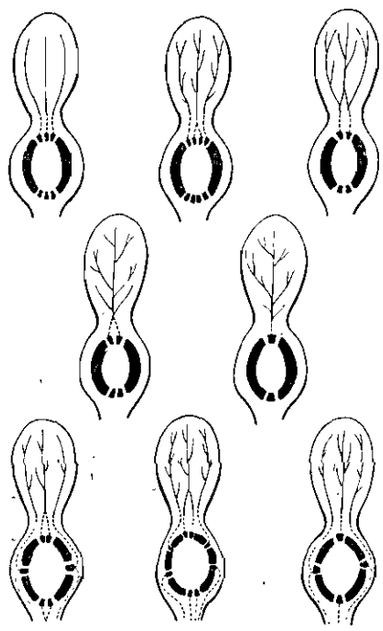

FIG. 78. Different types of vascularization of the cotyledonary node in dicotyledons. The most common type of cotyledonary node in the 99 dicotyledonous families that have been investigated is the unilacunar node with two traces. (Adapted from Bailey, 1956.)

Bailey is of the opinion that the leaves of angiosperms are able to undergo reversible changes in shape and vascularization.

In the light of the above facts it can be assumed: (1) that the unilacunar node of certain genera of the Ranales is primitive and has not changed during its evolution, from that of the lower Pteropsida; (2) in certain other dicotyledonous genera, e.g. genera of the Leguminosae, Anacardiaceae and others, the unilacunar node has apparently been derived,

by reduction, from a trilacunar node; (3) there are positive indications in certain dicotyledonous groups, such as the Epacridaceae and Chloranthaceae, that in the course of evolution the tri- and multilacunar nodes have arisen from the unilacunar node (Bailey, 1956).

The evolutionary development from a unilacunar node with two leaf-traces to other types of unilacunar nodes with one, three, or more traces may occur in a single family as can be demonstrated in the Chenopodiaceae (Bisalputra, 1962; Fahn and Broido, 1963).

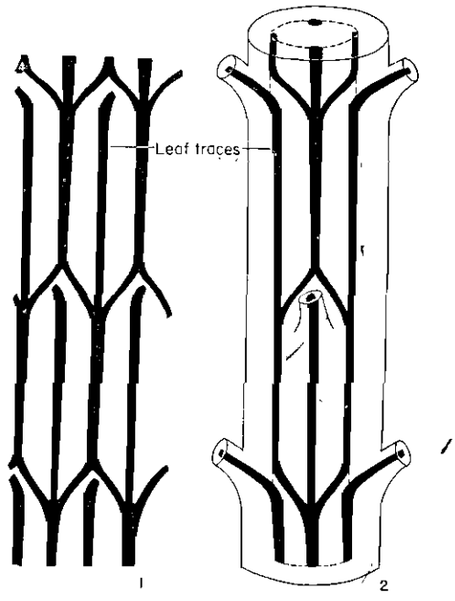

FIG. 79. Diagrams of the primary vascular system of the stem of *Anabasis articulata*. 1, Vascular system spread out on one plane. 2, Three-dimensional diagram showing the bundles on one side of the stem. The number of bundles and their arrangement as seen in cross-section can be seen at the level of the cut.

In order further to clarify the nature of the leaf-traces and the nodal type, it is necessary to study more accurately the nature of the traces and to follow their passage downwards in the stem. Often the picture obtained at the node is not a true reflection of the situation but lower in the stem the stele is more conservative (Fig. 76, no. 3) and a more correct picture of the arrangement of the leaf-traces is obtained (Fahn and Bailey, 1957). The suggested evolutionary trends of the basic types of nodal structure are given in Fig. 77, no. 5.

In the literature the bundles of the stem have been variously classified, i.e. as *leaf-trace bundles*, *cauline bundles* and *common bundles*. Leaf-trace

bundle was used to designate those bundles that directly connect the leaf and stele. Cauline bundle refers to those bundles that form the major vascular system of the stem and which may anastomose and give rise to leaf-traces. The term common bundle has been used for those bundles that run unbranched for a relatively long distance in the stem and which eventually terminate in a leaf-trace. However, it appears that in most plants the vascular system of the stem can be interpreted as being a system of leaf-traces that continue downwards in the stem for one or more inter-

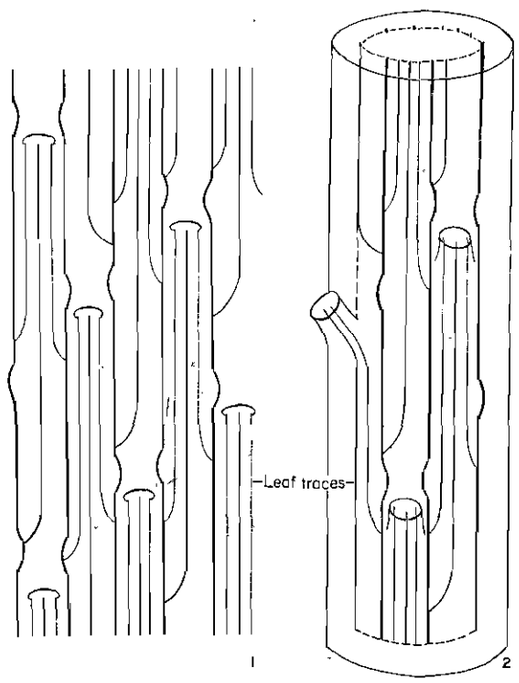

FIG. 80. Diagrams of the primary vascular system of the stem of *Chenopodium glaucum*. 1, Vascular system spread out on one plane. 2, Three-dimensional diagram showing the bundles on one side of the stem. The number of bundles and their arrangement as seen in a cross-section can be seen at the level of the cut.

nodes where they fuse with the leaf-traces of lower nodes (Figs. 79 and 80). This view is strengthened by the fact that the stem mainly functions as a connecting organ between the leaves and the root. The number of bundles in the stem is thus determined by the phyllotaxis and by the degree to which the traces continue down in the stem. Inasmuch as the phyllotaxis is more dense and the leaf-traces continue down along a larger num-

ber of internodes, the number of bundles, as seen in a cross-section of the stem, will be greater. Changes in number may sometimes occur along the stem of one plant. It is known, for example, that the number of bundles seen in a cross-section of that part of the stem that develops first, i.e. the lowermost portion, is less than that seen in cross-sections of higher portions, and that the number of bundles again decreases in the uppermost portion prior to the development of floral primordia.

BRANCH-TRACES

Branches develop from axillary buds and have vascular connections with the main axis. These vascular connections are termed *branch-traces.* At the node the branch-trace is situated very close to the leaf-traces that enter the leaf in whose axil the branch develops. The branch-gap is situated above the leaf-gap and together these two gaps appear as one. In the dicotyledons and gymnosperms the vascular supply to the axillary branches usually consists of two traces (Fig. 75, no. 2). However, in some plants only one trace is present and in others more than two. If only one trace is present in cross-section it appears horseshoe- or crescent-shaped. In the branches themselves, the stele is similar to that of the main axis.

SUMMARY OF THE ARRANGEMENT OF THE VASCULAR SYSTEM OF DICOTYLEDONS

The stems of the various dicotyledons differ from one another in the pattern of the primary vascularization (Balfour and Philipson, 1962, and others). These differences are apparently connected with evolutionary development.

The amount of primary vascular tissue, as has been described above, varies from a solid through a hollow uninterrupted cylinder to a small number of narrow separate bundles. It is assumed that during the course of evolution the primary vascular cylinder became thinner, i.e. it underwent reduction in a radial direction and because of the appearance of leaf-gaps, branch-gaps and perforations, and because of further reduction of the vascular tissue in a tangential direction, the cylinder became split into the longitudinal strands such as are seen in most dicotyledons.

The arrangement of secondary vascular tissue of the gymnosperms and dicotyledons bears no relation to the arrangement of the primary vascular tissue, and may be in the form of an entire cylinder. However, the amount and arrangement of the secondary vascular tissues and especially that of the xylem may also vary from an entire cylinder of various widths, as in trees, to separate strands, as in the herbaceous stems of certain annual

dicotyledons, e.g. *Cucurbita*, and in certain species it may even be almost completely absent. It is assumed that the reduction of the secondary vascular tissue is also the result of evolutionary processes.

VASCULAR SYSTEM OF MONOCOTYLEDONS

The vascular system of monocotyledons usually consists of bundles that are scattered throughout the ground tissue of the stem. In cross-sections of such stems it can be seen that the bundles do not form a ring such as is seen in cross-sections of most dicotyledons. Among dicotyledons, however, an arrangement of more or less scattered bundles does occur in a small number of plants, e.g. in the Nymphaeaceae, many plants of the Ranunculaceae and the herbaceous genera of the Berberidaceae.

In the Gramineae there are two basic types of arrangement of the vascular bundles: (1) that in which the vascular bundles are arranged in two circles (Fig. 81, no. 4), the outer circle consisting of thin bundles and the inner of thick bundles, e.g. *Triticum*, *Hordeum*, *Avena* and *Oryza*; and (2) that in which the vascular bundles are scattered throughout the entire cross-section of the stem, e.g. *Sorghum*, *Saccharum* and *Zea* (Fig. 81, no. 5). The individual bundles of the Gramineae are collateral and are usually surrounded by a sclerenchymatous sheath.

The complicated arrangement of vascular bundles in the monocotyledonous stem, and especially in the Gramineae, is connected with the position of the various bundles of each leaf in the stem. According to Kumazawa (1961) three types of leaf-trace bundles are present in the stem of *Zea* (Fig. 81, nos. 1, 2). The first type is represented by those bundles derived from mid-ribs and the larger lateral veins. These penetrate deep into the interior of the stem and then pass to the periphery in lower nodes. The second type is represented by leaf-trace bundles derived from smaller lateral veins which, immediately on entering the stem, occupy the position of the outermost peripheral bundles with which they fuse sooner or later. The third type is represented by bundles that are very thin and which soon fade out within the cortex close to the level of the node. It is important to mention that in the Gramineae there are special horizontal bundles at the nodes which connect the leaf bundles together (Fig. 81, no. 3).

In the stem of *Triticum* the internodes are hollow and the nodes solid. The thin leaf bundles are continued in the outer circle of the stem, and the thick bundles constitute the inner circle of bundles. Immediately above the position where the leaf is attached, the internodal vascular bundles become horizontal or oblique, and they approach the periphery. In the nodal portion the bundles branch and fuse in various ways, and this results in the reduction of their number. The remaining bundles, together with the thick bundles of the leaf of the same node, constitute the inner

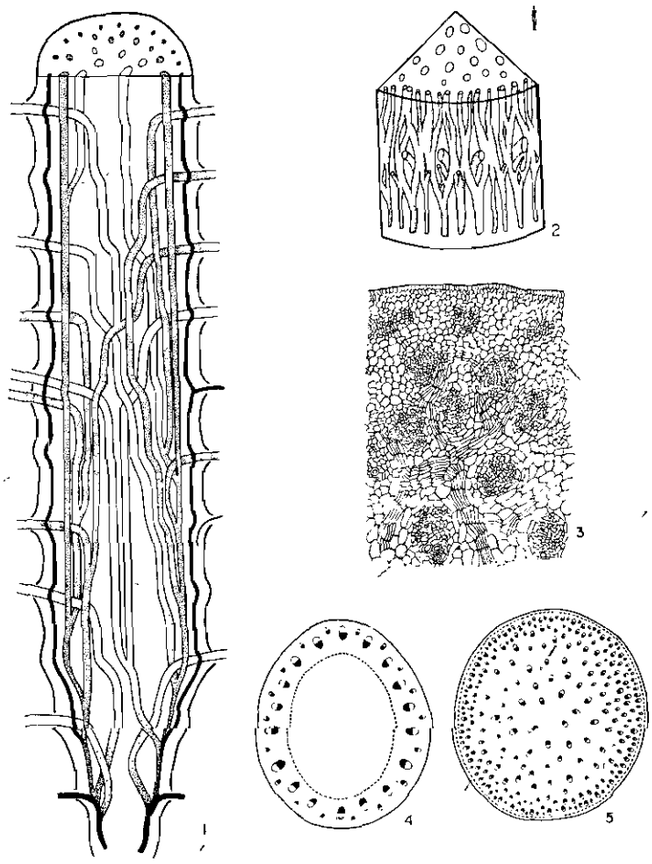

FIG. 81. 1–3, *Zea mays*. 1, Diagrammatic representation of a longitudinally sectioned stem showing the vascularization. Mid-rib leaf-traces—unshaded; large lateral leaf-traces—stippled; small lateral traces and very thin leaf bundles which fade out soon after entering the cortex—black. Coleoptile traces and the vascular system of the hypocotyl appear at the base of the diagram and are drawn in solid black. 2, Diagram of a reconstruction of part of a node. 3, Outer portion of cross-section of a young node showing the development of horizontal procambial strands which interconnect the vertical bundles. 4 and 5, Cross-sections of monocotyledonous stems showing two types of arrangement of the vascular bundles. 4, *Secale*, in which the vascular bundles are arranged in two rings. 5, *Zea mays*, in which the vascular bundles are scattered throughout the cross-section. (Nos. 1–3, adapted from Kumazawa, 1961; nos. 4–5, adapted from Troll, 1948).

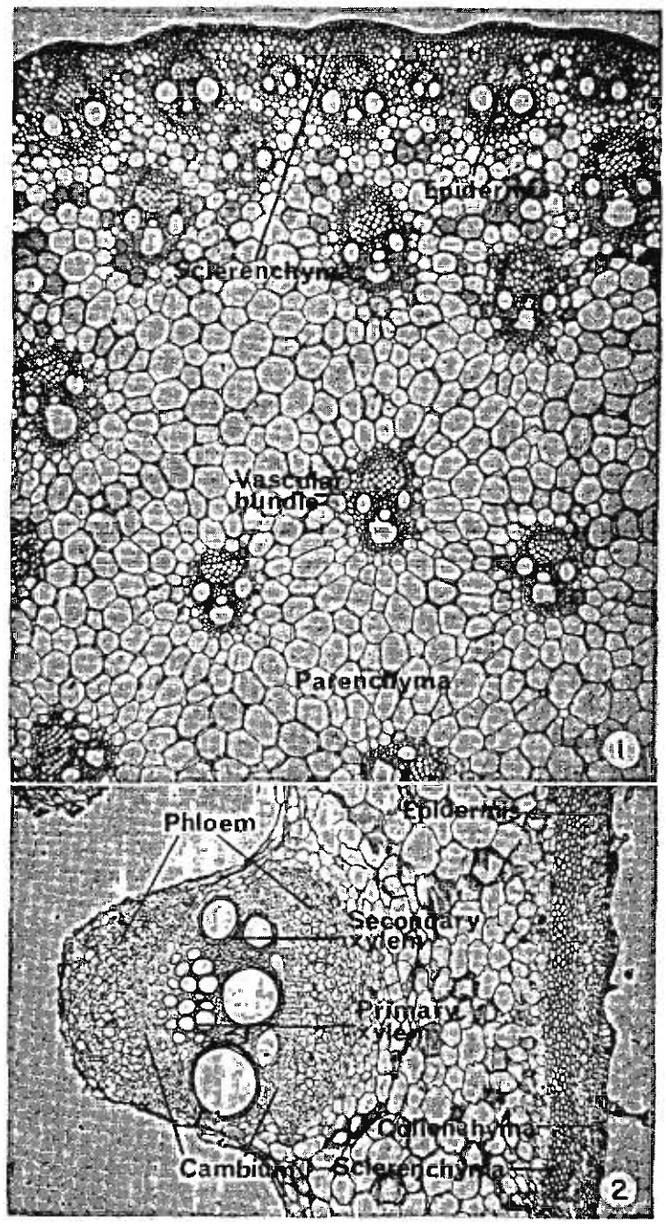

FIG. 82. 1, Micrograph of the outer portion of a cross-section of the stem of *Zea mays* showing the vascular bundles scattered in the ground parenchyma. ×50.
2. Portion of a cross-section of *Cucurbita* in which

circle of bundles of the next lower internode. In this circle, therefore, about half the bundles are those of the nearest leaf above the internode while the rest are from that internode above this leaf. Of the outer circle of an internode most of the bundles belong to the nearest leaf above it (Esau, 1953).

ONTOGENY OF THE PRIMARY VASCULAR SYSTEM

With the progressive differentiation of the promeristematic cells the three meristems, the protoderm, ground meristem and procambium, are formed. The procambium may be in the form of a solid or hollow cylinder or of strips. The procambium stains more intensely than the neighbouring tissues as a result of the delayed appearance of the vacoules in it. The development of the procambium is continuous in an acropetal direction, i.e. from below towards the apex. The procambium differentiates below the position where a leaf primordium is formed as a small buttress on the surface of the apex. As the leaf primordium grows its procambium develops in continuation with the procambial strands of the stem below it. Various opinions exist as to what factors control the order of appearance of leaves, their arrangement and the organization of the apex, in general. Some workers regard the controlling centre as being in the promeristem of the apex, while others regard it as being in the procambium which develops acropetally (Crafts, 1943; Gunckel and Wetmore, 1946a, b; Snow and Snow, 1947; Philipson, 1949; Wardlaw, 1948, 1950, 1955).

The differentiation of procambial cells into cells of the vascular tissue takes place in different plants and organs at different stages of procambial development. For instance, in aerial stems of the spermatophytes the procambial cells undergo differentiation into tracheary elements even at the level where cell division still takes place in the procambium, while in the roots of most spermatophytes and in the stems of most pteridophytes the first differentiation of the procambium takes place only where almost all of the procambium cells have ceased to divide.

The earliest sieve elements (those of the protophloem) usually undergo acropetal differentiation, i.e. from the phloem of the traces of more mature leaves, to the leaf primordia. The development of the phloem commences before the appearance of the xylem elements. In spermatophytes the primary xylem begins to differentiate from the procambium near the base of the developing leaf, from where its further differentiation continues in two directions—acropetally into the leaf, and basipetally into the stem. In the stem the newly formed xylem becomes continuous with the xylem of earlier formed strands.

The above processes of differentiation have been proved only in relation to the development of the protophloem and protoxylem. As yet the pattern

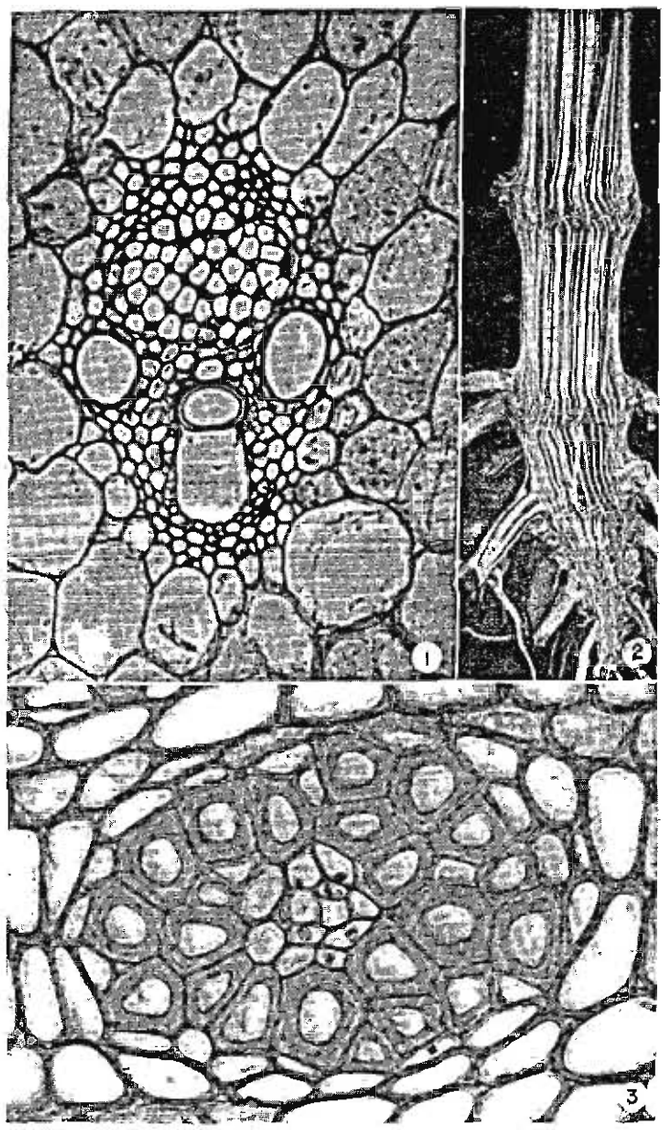

FIG. 83. 1, Micrograph of a cross-section of a single vascular bundle of *Zea mays*. ×200. 2, Photograph of the lower portion of a longitudinally sectioned mature stem of *Zea mays* in which most of the parenchymatous tissues have been destroyed and showing horizontally orientated vascular bundles at the nodes. 3, Micrograph of a cross-section of an amphivasal secondary vascular bundle from the stem of *Dracaena* ×420.

of differentiation of the metaphloem and metaxylem along the shoot has not been investigated thoroughly in the spermatophytes.

In the procambium it is possible to distinguish between that part that will differentiate into xylem and that part that will differentiate into phloem by the more intense staining of the latter as well as by the differences in the plane of cell division.

According to the sequence of differentiation of the xylem across that part of the procambium from which the xylem develops, three types of xylem can be distinguished.

1. The type in which the first-maturing elements are external, i.e. closest to the periphery of the organ, as is seen in angiosperm roots (Fig. 114, no. 1). In this type the direction of the maturation of the xylem elements is centripetal. This type of xylem is termed *exarch.*

2. The type in which the first-maturing elements are internal, i.e. nearest to the centre of the axis, as is seen in angiosperm stems (Fig. 71). In this type the direction of the maturation of the xylem elements is centrifugal. This type of xylem is termed *endarch.*

3. The type in which the first-maturing elements occur in the middle of the xylem strand. In this case the direction of the maturation of the xylem elements is both centripetal and centrifugal. This type of xylem is termed *mesarch.*

The exarch and mesarch types of primary xylem are apparently the more primitive.

The phloem always develops towards the xylem. In those cases where the phloem is situated only on the outside of the xylem the development of the phloem is centripetal, and in internal phloem the development is centrifugal.

In plants that exhibit secondary thickening that part of the procambium between the primary xylem and phloem remains meristematic and forms part of the vascular cambium.

Adaptation of the stem to desert and saline habitats

In desert perennials the leaves are usually very much reduced, e.g. as in the articulated Chenopodiaceae, or they are shed at the beginning of the very long dry season. In some plants, e.g., *Artemisia* spp., *Reaumuria* spp., *Gymnocarpos fruticosus* and *Atriplex* spp., the shed leaves are replaced, during the dry season, by smaller and more xeromorphic leaves (Zohary, 1961). In other plants, e.g. *Zygophyllum dumosum,* the chloroplast-containing petioles are retained after the leaflets are shed. In still others, such as *Retama raetam* and *Calligonum comosum,* in which the function of photosynthesis is taken over by the young green branches, these branches may be shed. In many desert plants even ordinary branches and larger portions

of the plants die during the dry season (Orshan, 1953) so reducing the plant body and its requirements to a minimum. However, although most desert perennials appear dead at the end of the dry season they are capable of developing new shoots with the onset of the rainy season.

As no or little foliage actually remains on desert plants during the dry season, the main problem of adaptation is not by what means transpiration is reduced in the leaves, but how the plant remains viable until the onset of the rainy season. The answer to this question must therefore be sought in the axis of the plant.

In some desert plants the function of photosynthesis is taken over by the cortex of the stem. In others, in addition to the presence of photosynthesizing tissues, water-storing parenchyma, is developed.

Another commonly observed character of desert shrubs is the occurrence of a split axis. The axes of *Artemisia herba-alba*, *Peganum harmala*, *Zygophyllum dumosum* and *Zilla spinosa*, for instance, become split by various anatomical mechanisms into separate parts or "splits" (Ginzburg, 1963) which may compete with one another; the split in the most favourable microhabitat around the mother plant will probably be the one to survive.

In primary stems the cortex is generally narrow and the vascular tissues are situated on the periphery of a wide pith. However, it has been observed that the cortex of the primary stem of plants growing in deserts or salt marshes is recognizably thicker than in mesophytes. This feature, which is accompanied by the "contraction" of the vascular strands around a narrow pith, may be an adaptive one by which the vascular tissues are protected from drought or other damage in the early stages of development before the periderm is developed.

It is known that in the articulated Chenopodiaceae, such as *Anabasis* spp., *Haloxylon* spp. and *Arthrocnemum glaucum*, the fleshy photosynthesizing cortex is shed from the mature stems in the summer as the result of the formation of a periderm which develops in the phloem parenchyma (Fahn, 1963). It is also of interest that in some desert plants, such as *Atriplex halimus*, *Zygophyllum dumosum* and *Fagonia cretica*, for example, which do not have a fleshy cortex, the first-formed periderm also develops deep within the stem in the pericycle or phloem parenchyma. This is an adaptive feature.

In some desert shrubs, such as *Artemisia* spp. and *Achillea fragrantissima*, interxylary cork rings are produced at the end of each annual wood increment. Moss (1940) has already pointed out the important adaptive value of these interxylary cork tissues which reduce water loss and restrict the upward passage of water to a narrow zone of functioning secondary xylem.

The anatomical structure of the stems of some *xerophytes* (plants growing in arid habitats) and one *halophyte* (plant growing in saline soil) will be described here.

Retama raetam. (Fig. 84, no. 3) may be cited as an example of plants with xeromorphic stem (Evenari, 1938). Along the green branches of this plants there are ribs and furrows. The stomata are situated in the furrows in which there are also numerous hairs. The central portion of the ribs consists of a sclerenchymatous strand which is accompanied laterally, on the sides facing the furrows, by one or two rows of large colourless parenchyma cells which serve as water-storing cells and usually contain crystals. Be-

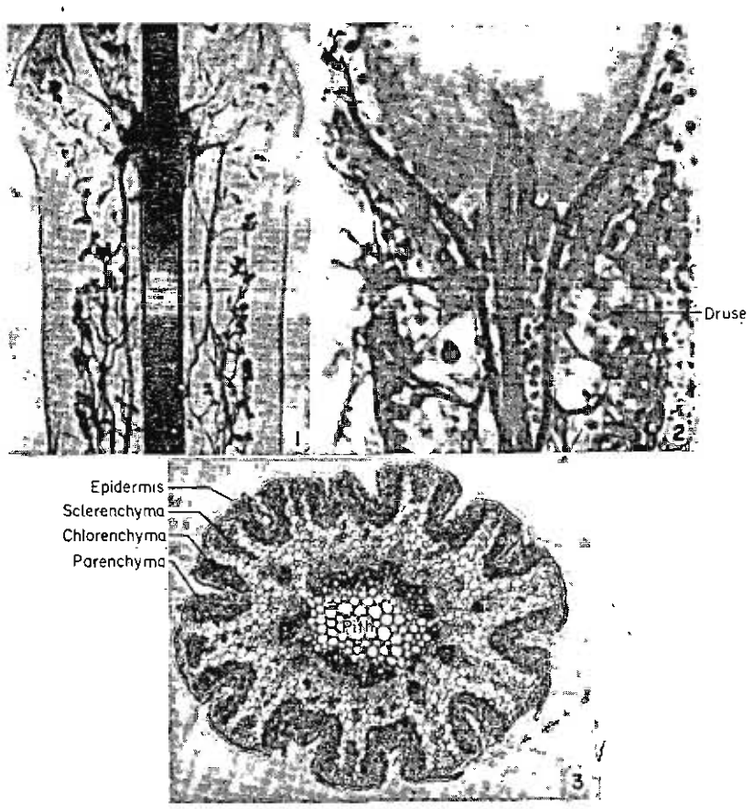

FIG. 84. Succulent and xeromorphic stems. 1, *Arthrocnemum glaucum*. Portion of cleared young stem showing the vascular system to be contracted to a narrow cylinder in the centre of the stem and the anastomosing system of vascular bundles in the fleshy cortex and reduced leaves. ×12. 2, Portion of a cleared fleshy young stem of *Anabasis articulata*, from which the epidermis has been removed; in addition to the details distinguishable in no. 1, numerous crystals in the form of druses can be seen. ×27. 3, Micrograph of a cross-section of a young stem of *Retama raetam* in which the ribbed nature of the cortex can be seen. ×30.

tween these cells and the epidermis is the photosynthesizing tissue, which consists of small and dense parenchyma cells containing chloroplasts and crystals. The epidermal cells have very thick outer walls and cuticle.

The *succulent stems* of desert plants are characterized by a well developed water-storing tissue in the cortex and pith. As a result of this the ratio between the cortex and vascular cylinder in these plants is considerably larger than that of other dicotyledons (Fig. 84, nos. 1,3). *Anabasis articulata* (Fig. 84, no. 2; Fig. 85) may be cited as an example of desert plants with a

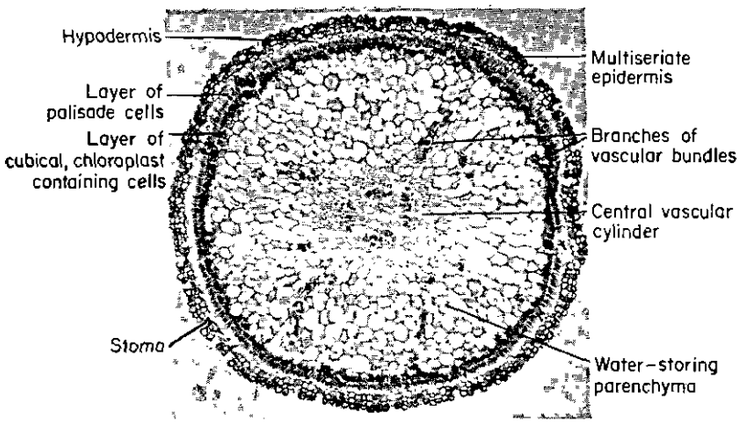

FIG. 85. Micrograph of a cross-section of the stem of *Anabasis articulata*. ×28.

succulent stem (Volkens, 1887; Evenari, 1938; Fahn and Arzee, 1959). In the young green internodes the epidermis consists of three to four layers of thick-walled cells and it is covered by a very thick cuticle. Below the epidermis is a hypodermis of thinner-walled cells which similarly to the epidermis contain crystals. On the inside of this layer there is a layer of palisade cells with chloroplasts. Immediately inside the palisade tissue is a layer of more or less cubical cells which also contain chlorophyll. Still further inwards is the water-storing parenchyma which also contains, here and there, large druses. With the maturation of the stem, cork tissue develops in the outer phloem parenchyma. Branches of the vascular bundles of the internodes pass through this cork tissue into the cortex. In still older branches the connection between the bundles and their branches is disrupted by the completion of the cork cylinder and, as a result, the outer layers dry out and are shed.

In *Salicornia fruticosa* (Fig. 86, nos. 1–3) which grows in salines, the structure of the cortex is simpler (Fahn and Arzee, 1959). The epidermis

is single-layered and thin-walled. The photosynthesizing tissue consists of large palisade cells which store water, as do the parenchyma cells of the inner cortex.

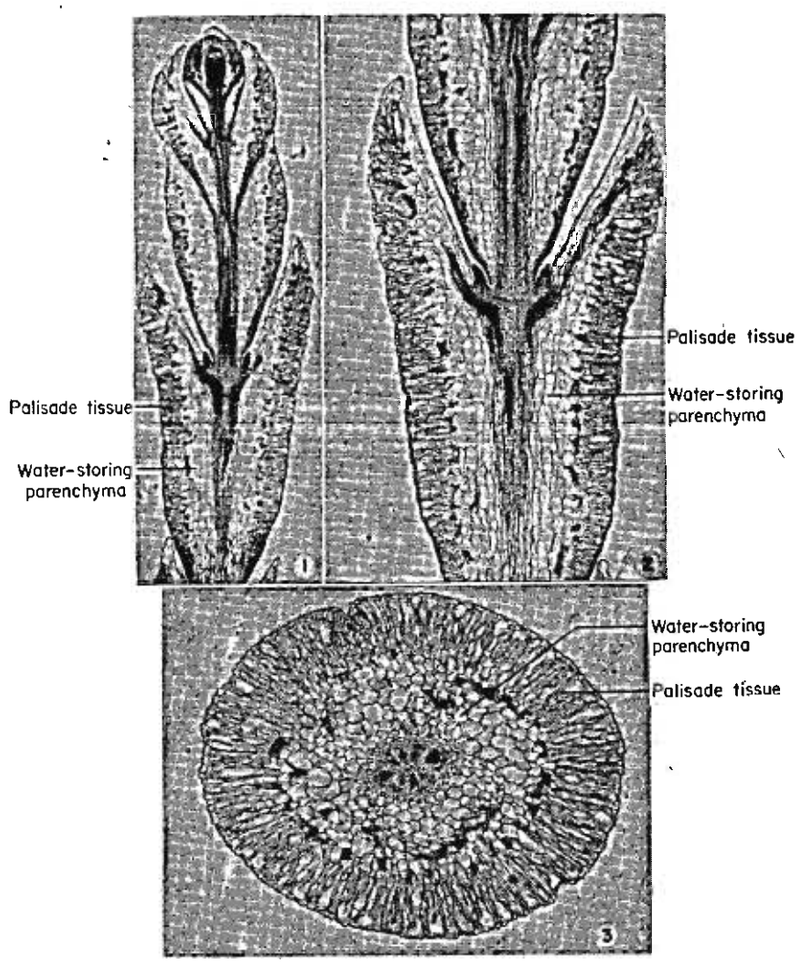

FIG. 86. Succulent articulated stem of *Salicornia fruticosa*. 1, Longitudinal section of the upper portion of the stem. ×13. 2, Portion of no. 1, enlarged. ×20. 3, Cross-section of an internode. ×30.

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CHAPTER 12

THE LEAF

As has already been mentioned, it is difficult, both from theoretical and practical viewpoints, to distinguish clearly between the leaf and the stem. This difficulty is clarified in the light of the accepted assumption that the leaves in the Pteropsida (the higher Pteridophyta and the Spermatophyta) have, phylogenetically, developed from a certain system of branches.

The structure of the conducting tissues in the petiole and main vein of the leaf is usually similar to that of the stem. Sometimes the same photosynthetic and non-photosynthetic parenchymatous tissues are found both in the leaves and in the cortex of the stem (Fahn and Arzee, 1959). The most important characteristic of the leaf is the early termination of apical growth. In certain ferns the apical meristem remains active for a relatively long period, while in other ferns, e.g. *Ophioglossum*, and in the Spermatophyta the true apical activity ceases very early in the development of the leaf and then the shape and size of the leaf is determined by intercalary and marginal growth.

Morphologically and anatomically the leaf is the most variable plant organ. The collective term for all the types of leaves appearing on plants is the *phyllome* (Arber, 1950). The different phyllomes of the Spermatophyta are extremely variable both in external and in internal structure and in function. Because of this variability the following types of phyllomes have been classified: *foliage leaves*, *cataphylls*, *hypsophylls*, *cotyledons*, and others. The foliage leaves are the principal photosynthetic organs. The cataphylls are the scales that appear on buds and on underground stems and their function is protection or the storage of reserve materials. The first, lowermost leaves of a side branch are termed *prophylls;* in monocotyledons only one prophyll is usually present and in dicotyledons, two. The hypsophylls are the various types of bracts that accompany the flowers and their function is, apparently, protection. Sometimes the hypsophylls are coloured and then their function is similar to that of petals. The cotyledons are the first leaves of the plant. The floral organs are also considered as leaves.

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Morphology of the leaf

In this chapter we shall deal with foliage leaves which, among the Angiospermae in particular, themselves exhibit great variation in anatomical and morphological structure. The foliage leaves in certain angiosperm genera are sessile and consist almost entirely of lamina, but in most genera several distinct parts can be distinguished in the foliage leaf, i.e. the *leaf base*, *petiole* and *lamina*. The shape, structure and relative size of these parts differ and are used to classify the foliage leaves into different types. In many dicotyledonous genera two appendages, i.e. the *stipules*, develop at the leaf base. The stipules may be attached to the leaf base or they may be free appendages. Even when they are free appendages they develop as outgrowths of the leaf primordia. The vascular supply of the stipules is derived from the leaf traces (Fig. 97, no. 2). In some plants the stipules are green and resemble leaflets and have a photosynthetic function, but their main function is the protection of young developing leaves. In some

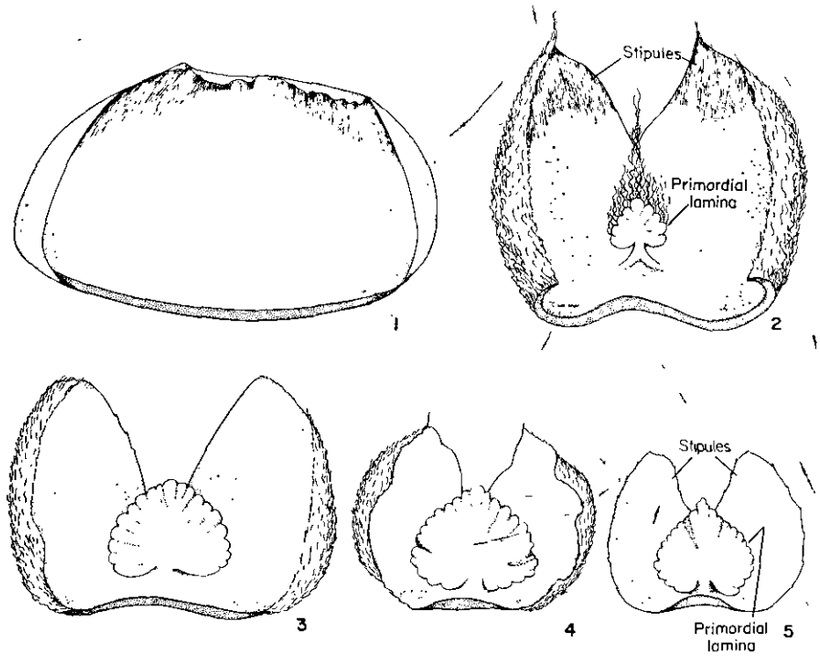

FIG. 87. Bud scales of *Vitis vinifera*. Numerals indicate the centripetal order of appearance of the scales and young foliage leaves. 1, Cataphyll which envelops the bud. 2–5, Young foliage leaves in order of their appearance in the bud. The stipules of the outer leaves are relatively large and they serve to protect the bud. (Adapted from drawings made by Z. Bernstein.)

woody dicotyledons (e.g. *Ficus* and *Vitis*) the outermost scales protecting the buds are stipules (Fig. 87, nos. 1–5). In most monocotyledons and some dicotyledons (the Umbelliferae and Polygonaceae) the leaf base is widened so as to form a *sheath* which surrounds the node. Usually a relationship exists between the anatomical structure of the node and the appearance of stipules and a sheath in the dicotyledons (Sinnott and Bailey, 1914). Most plants with trilacunar nodes (i.e. those in which there are three leaf-gaps at each node) have stipules and those with multilacunar nodes, have sheath-like leaf bases.

Leaves are divided into *simple* and *compound* depending on whether the stalk bears one or more leaflets. In the case of compound leaves the common stalk is termed the *rachis*. If the leaflets arise from the sides of the rachis, the leaf is said to be *pinnate*, and if all from one point, as rays, *palmate*. The margin of the leaf, and similarly the leaflets, may be entire or variously notched.

In some plants, such as many species of *Acacia* of Australian origin, the lamina of the leaves is reduced, and from the remaining parts a flat, leaf-like photosynthetic organ is developed; this type of organ is termed a *phyllode*. In certain plants (*Opuntia* spp., *Muehlenbeckia platyclados*) the stems are photosynthetic and have become flat; such organs are termed *platyclades*. When the platyclade appears very leaf-like, as in *Ruscus*, it is called a *phylloclade*.

Histology of the foliage leaf

Histologically the leaf is composed of three types of tissue systems: epidermis, mesophyll and vascular tissues.

THE EPIDERMIS

The epidermis of leaves of different plants varies in the number of layers, its shape, structure, arrangement of the stomata, appearance and arrangement of trichomes and occurrence of specialized cells. (The above features are discussed in Chapter 10.) Because of the usually flat structure of the leaf, a distinction is made between the epidermal tissues of the two surfaces of the leaf; that surface of the leaf that is closer to the internode above it and which usually faces upwards is referred to as the *adaxial surface*, and the other surface as the *abaxial surface*.

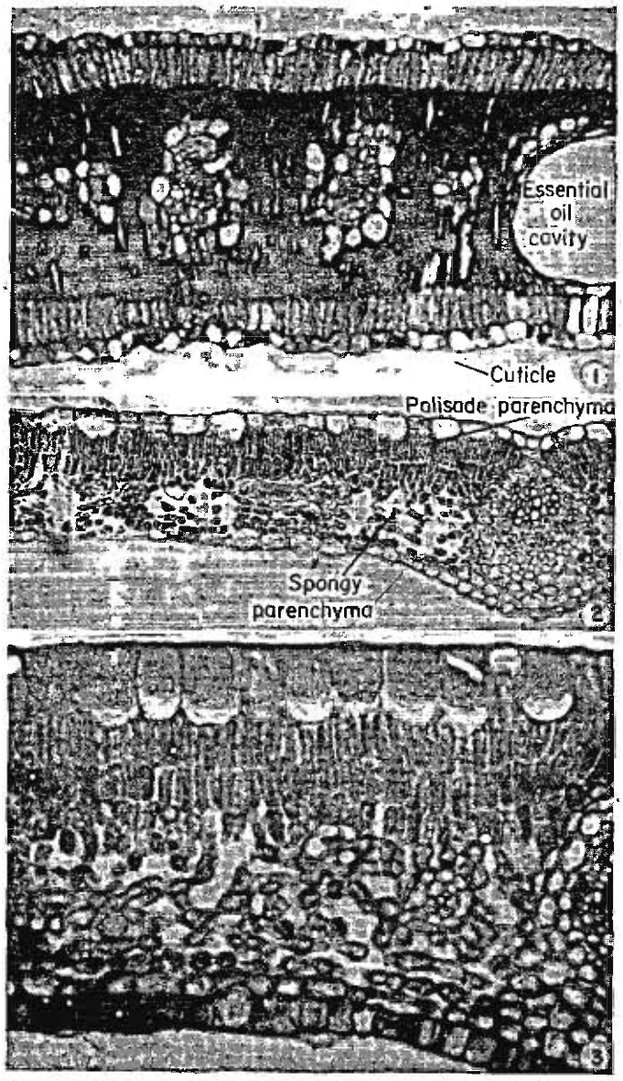

FIG. 88. Micrographs of portions of cross-sections of leaf laminae. 1, *Eucalyptus hemiphloia* which has an isolateral arrangement of mesophyll tissues and a thick cuticle. The inner palisade-like cells are darkly stained because they contain tannins. Bundle sheaths surrounding the veins can be distinguished. ×130. 2, *Rosa* showing the dorsiventral arrangement of the mesophyll. ×140. 3, As in no. 2, but portion enlarged. ×270.

THE MESOPHYLL

The mesophyll comprises the parenchymatous tissue internal to the epidermis. The mesophyll usually undergoes differentiation to form the photosynthetic tissues and so contains chloroplasts. In many plants, especially among the dicotyledons, two types of parenchyma can be distinguished in the mesophyll: *palisade parenchyma* and *spongy parenchyma* (Fig. 88, no. 3; Fig. 91, nos. 1, 2). The cells of typical palisade parenchyma are elongated and in cross-section of the leaf they are rod-shaped and appear to be arranged in rows, while in a section parallel to the leaf surface these cells are seen to be rounded and separated or only slightly attached to one another (Fig. 91, no. 1). In certain plants the palisade cells are of shape different from the typical. In certain species of the Xanthorrhoeceae small papilla-like projections and constrictions which run around the cells are found (Fahn, 1954). In *Lilium* large lobes are present on the palisade cells which therefore appear branched (Fig. 89, no. 1).

The palisade cells are found immediately below the uni- or multiseriate epidermis, but sometimes a hypodermis may be present between the epidermis and the palisade tissue. The cells of palisade parenchyma may be arranged in one or more layers and in the latter case the length of the cells in the different rows may be equal, or they may become shorter towards the centre of the mesophyll. The palisade tissue is usually found on the adaxial surface of the leaf. In some plants, however, e.g. *Thymelaea*, the palisade parenchyma is found only on the abaxial side of the leaf (Fig. 89, nos. 2, 3). In certain plants, including many xeromorphic species, e.g. *Dianthus caryophyllus*, *Atriplex portulacoides* (Fig. 90, no. 1), species of *Centaurea*, *Artemisia* and *Myoporum*, palisade parenchyma is present on both sides of the leaf with the result that only a small strip of spongy parenchyma is present in the central portion of the lamina. A leaf in which the palisade parenchyma occurs on one side of the leaf and the spongy parenchyma on the other is termed *dorsiventral* or *bifacial*. When the palisade parenchyma is present on both sides of the leaf, the leaf is said to be *isolateral* or *isobilateral*.

The cells of the spongy parenchyma are variously shaped. They may resemble the palisade cells, or have equal diameters, or be elongated in a direction parallel to the leaf surface. However, a characteristic of all spongy parenchyma cells is the presence of lobes by which the neighbouring cells are connected.

The distinction between the palisade and spongy parenchyma is not always easy, especially when the palisade parenchyma consists of several layers. In the latter case the cells of the innermost layers greatly resemble those of adjacent spongy parenchyma.

In certain plants, such as *Zea* and many other grasses, the mesophyll cells are more or less uniform in shape (Fig. 93, no. 2). Also in certain

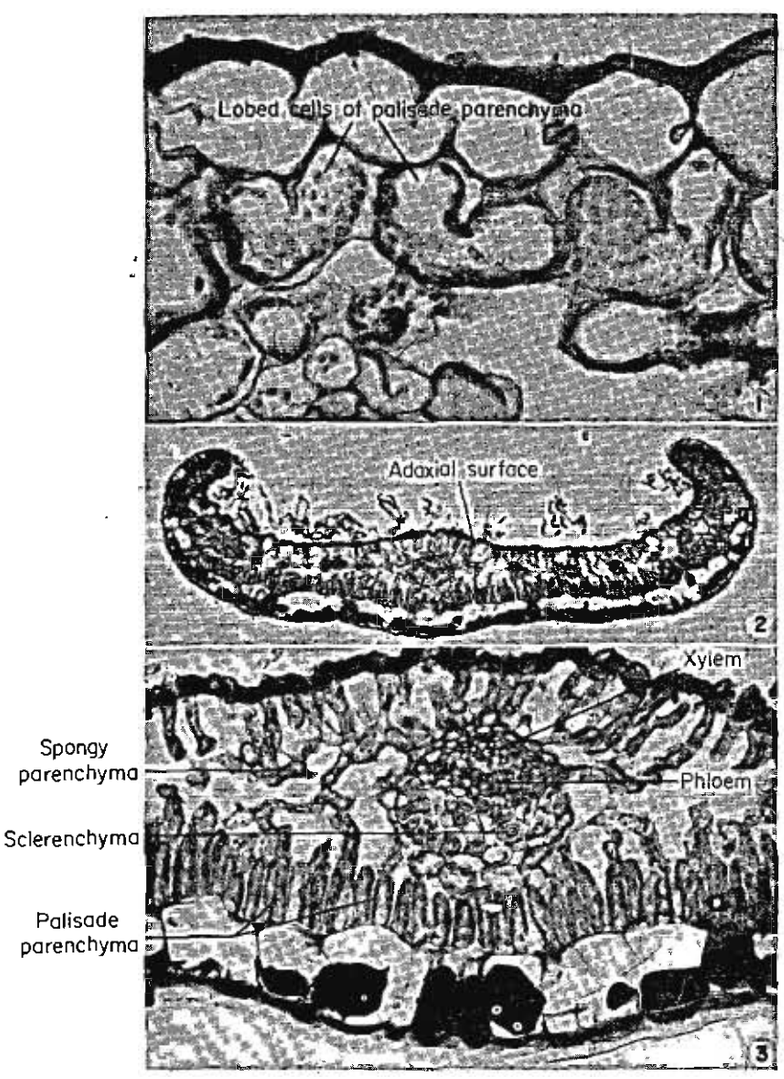

FIG. 89. 1, Portion of a cross-section of the lamina of *Lilium candidum* showing lobed palisade parenchyma cells immediately below the epidermis. ×430. 2, Cross-section of the leaf of *Thymelaea hirsuta* in which the palisade parenchyma is present on the abaxial side of the leaf and the spongy parenchyma on the adaxial side. ×55. 3, As in no. 2, but portion around mid-rib enlarged. ×200.

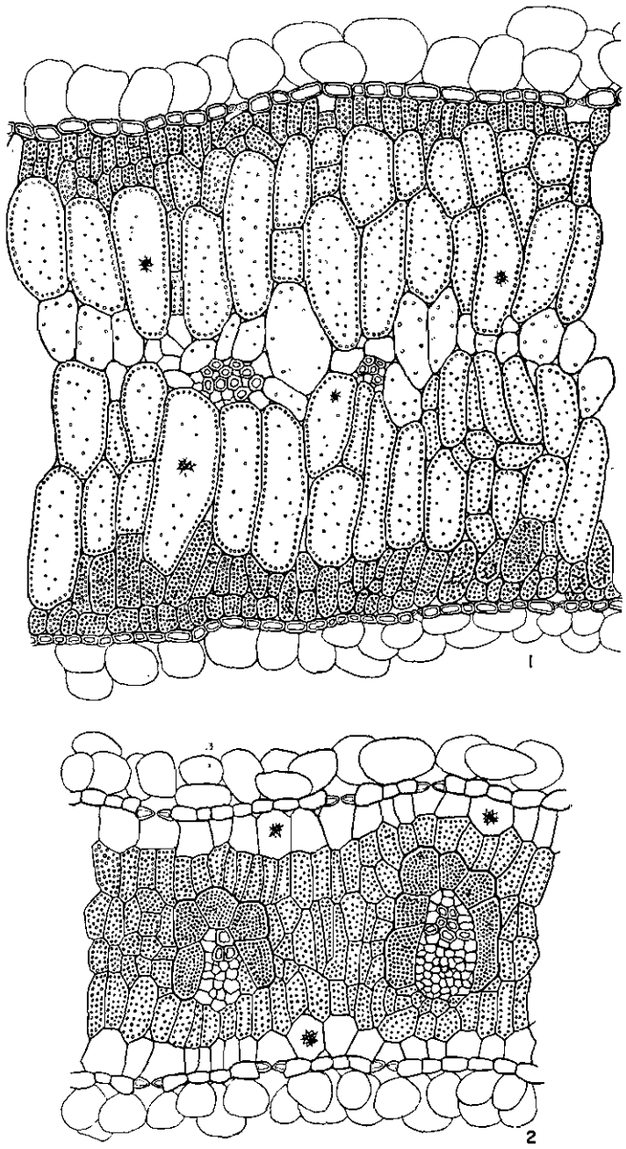

FIG. 90. 1, Portion of a cross-section of the leaf of *Atriplex portulacoides* showing the vesiculate salt trichomes, thick-walled epidermis and isobilateral arrangement of the mesophyll tissues. The inner mesophyll cells are large, contain few chloroplasts and store water; occasional druses occur in these cells. 2, As above, but of *Atriplex halimus* in which the epidermis is relatively thin-walled, the uniseriate hypodermis is devoid of chloroplasts, stores water and contains occasional druses. The chlorenchyma, which consists of uniform elongated cells, is present between the abaxial and adaxial hypodermal layers. The bundle sheaths are open on the abaxial side of the veins and the cells of the

species of *Eucalyptus* (e.g. *E. hemiphloia*) and in *Atriplex* it is not possible to distinguish between two types of parenchyma, and the mesophyll is entirely composed of palisade cells (Fig. 88, no. 1; Fig. 90, no. 2).

The palisade tissue has become specialized in such a way that the efficiency of photosynthesis has been increased. In mesophyll that can be clearly divided into palisade and spongy parenchyma the large majority of the chloroplasts are found in the palisade cells. Because of the shape and arrangement of the palisade cells the chloroplasts can be placed so as to

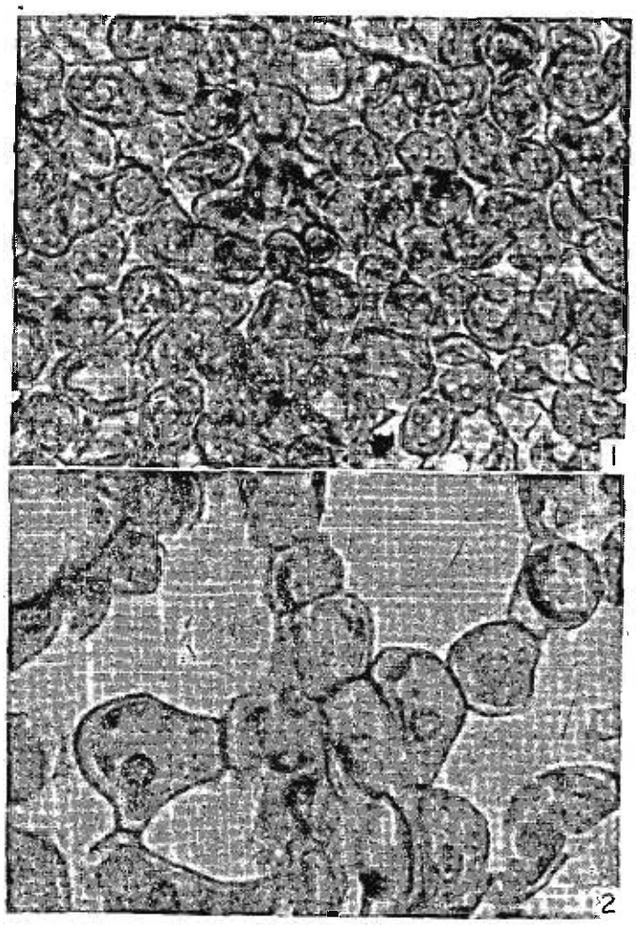

FIG. 91. Micrographs of sections cut parallel to the leaf surface of *Rosa*. 1, Section through the palisade parenchyma. ×520. 2, Section through spongy parenchyma. ×420.

enable the maximum utilization of light. Under illumination the chloroplasts form a single layer lining the walls of the palisade cells.

Another important factor that increases photosynthetic efficiency is the presence of a well developed system of intercellular spaces which is present in the mesophyll, and which facilitates rapid gas exchange. Because of the cell arrangement in the mesophyll large surface areas of the cells are exposed and so brought into contact with air. Together these surface areas have been termed the *internal surface area* of the leaf as distinct from the

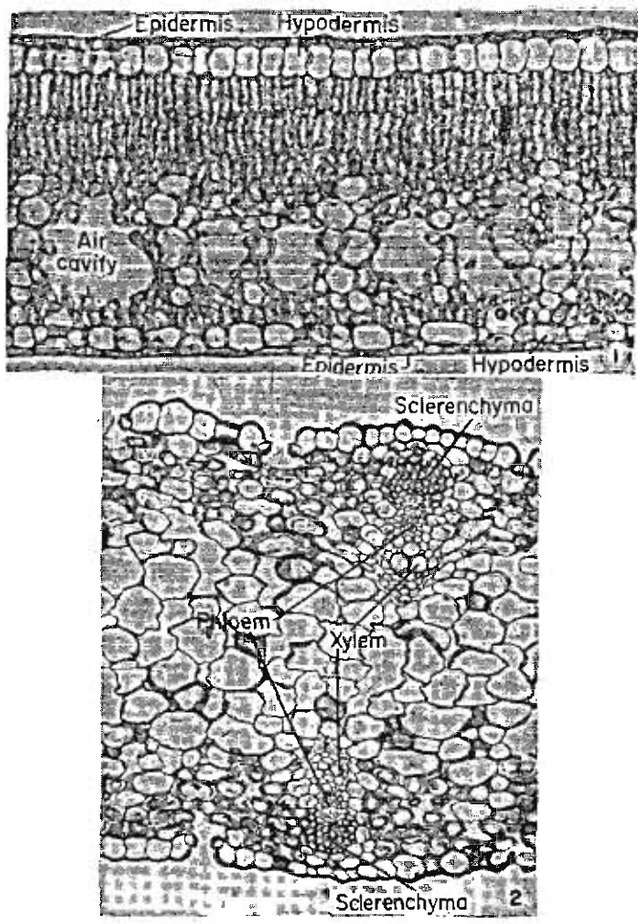

FIG. 92. Micrographs of portions of cross-sections of leaf laminae. 1, *Musa* (Dwarf Cavendish banana). ×150. 2, *Iris*, in which the leaf is unifacial. ×100.

external surface area of the leaf. The ratio of the volume of the intercellular spaces to the total volume of the leaf varies between 77 : 1000 and 713 : 1000 (Sifton, 1945). The ratio of the internal surface area to the external surface area is of ecological importance (Turrell, 1936, 1939, 1942, 1944). The internal surface area of *Styrax officinalis* is eight times larger than the external surface area, and in *Olea* it is eighteen times larger.

The specialization of the palisade tissue that results in more efficient photosynthesis is brought about not only by the increased number of chloroplasts in the cells but also by the dimensions of its free surface area. Although the volume of the intercellular spaces in the spongy tissue is much larger than that in the palisade tissue, the free surface area is greater in the palisade tissue. This feature becomes obvious when sections parallel to the leaf surface are examined (Fig. 91, nos. 1, 2). In such sections it is seen that the palisade cells are round in cross-section and that the areas of contact between the cells are restricted to very narrow strips, while the areas of contact in the spongy tissue are flatter and wider. Thus, for example, in *Styrax officinalis* the free surface area of the palisade tissue is about twice as large as that of the spongy tissue.

The intercellular spaces of the mesophyll usually develop schizogenously, but in certain plants the development may also be lysigenous by the disintegration of groups of cells. Examples of the latter type of development are seen in water and marshy plants, and also in the banana leaf (Skutch, 1927) (Fig. 92, no. 1).

STRUCTURAL CHANGES OF EPIDERMIS AND MESOPHYLL IN LEAVES OF XEROPHYTES

Xerophytes, according to the definition of Maximov (1931), are plants that grow in arid habitats and whose transpiration decreases to a minimum under conditions of water deficiency. Plants may develop structural characteristics that are adaptations to arid habitats. Such plants are termed xeromorphic plants. Xeromorphism, however, is not confined to xerophytes, and not all xerophytes exhibit xeromorphic characters.

One of the most obvious features of xeromorphic leaves is the small ratio of the external leaf surface to its volume. According to numerous workers (Schimper, 1898; Maximov, 1929; Weaver and Clements, 1929; Oppenheimer, 1960, and others) the reduction of the external surface is accompanied by certain changes in the internal structure of the leaf as, for instance, the reduction in cell size, the increase in the thickness of the cell walls, the greater density both of the vascular system (Wylie, 1949) and of the stomata, and the increased development of the palisade tissue at the expense of the spongy tissue. Xeromorphic leaves are often covered with trichomes. In xerophytes with succulent leaves water-storing tissue is developed.

The lack of nitrogenous compounds and/or water in the soil often results in the appearance of xeromorphic characters such as the formation of thick walls and cuticle and the additional development of sclerenchyma (Volkens, 1887; Kraus and Kraybill, 1918; Welton, 1928; Schneider, 1936). A clear relationship can be established between the salinity of the soil and the appearance of succulent features in the plants growing in it (Mothes, 1932). Intense illumination and the retardation of the water flow due to water deficiency apparently results in the increased development of palisade tissue (Shields, 1950).

Some of the above changes, such as the increase in the number of stomata, allow a higher rate of gas exchange under conditions of favourable water supply. Furthermore, the increased development of palisade tissue probably results in an increase of photosynthetic activity.

The reduction in the size of the leaf is thought to be a feature correlated with the reduction of the rate of transpiration and in many places it is seen that plants with small leaves are commoner in dry habitats. In some cases the reduction of leaf size is connected with an increase in the total number of leaves on the plant. Thus, for example, the total external surface area of the entire foliage of certain coniferous trees is usually greater than that of many dicotyledons (Groom, 1910).

Trichomes are very common on xerophytes. If a species exists in both xeromorphic and mesomorphic forms, the former has a denser indumentum (Coulter *et al.*, 1931). In many xeromorphic plants, such as, for instance, *Nerium* and *Xanthorrhoea*, the stomata are sunken in depressions or grooves which are covered by trichomes (Fig. 93, no. 1).

According to some investigators (such as Weaver and Clements, 1929), the trichomes and wax coverings play but a small role in the reduction of transpiration as long as the stomata are open. However, when the stomata are closed these structures fulfill an important protective function. According to Shields (1950), living trichomes, which themselves lose water, do not protect the plant from excessive transpiration as do dead trichomes which form protective layers. As trichomes are more numerous on plants growing in dry habitats, and as they do not prevent excessive evaporation, Shields suggests that it is possible that the trichomes are symptoms of water loss rather than being structures that function to reduce evaporation.

Volkens (1887) suggested that in some desert plants the stomata on the photosynthesizing plant organs become permanently closed during the summer season. This closure is caused by the additional thickening and cutinization of the guard-cell walls (e.g. *Aristida ciliata*, *Sporobolus spicatus*) or by the blocking of the sunken stomata from the exterior by resinous masses (e.g. *Pityranthus*) or by wax layers (e.g. *Capparis spinosa*). In *Anabasis articulata* and other related species prominent wall thickenings have been seen to develop in the guard cells in the hot summer months. The permanent closure of the stomata of desert plants during the dry sea-

son should be investigated experimentally, as this feature explains how those green parts of desert plants that do not dry out manage to retain their water content (Fig. 64, nos. 1, 2).

In *Rumex acetosella* drops of resin or oil form in the epidermis and in the cells around the veins under drought conditions (Transeau, 1904); this feature apparently hinders the passage of water. It is possible that this is also the function of the tannins and resins found in species of *Quercus* and *Pistacia* of the Mediterranean maquis.

Water in leaves is conducted not only by the veins and bundle-sheath extensions, but also by the mesophyll cells and epidermis (Shull, 1934; Wylie, 1943). Water transport towards the epidermis is much higher through the palisade tissue than through the spongy parenchyma. In centric xeromorphic leaves the palisade cells radiate around the central vascular bundles and therefore, under favourable conditions of water supply, the transport of water from the bundles to the epidermis is enhanced (Thoday, 1931). The presence of intercellular spaces, especially between the palisade cells, however, limits water transport in the plane parallel to the leaf surface (Wylie, 1943).

The volume of intercellular spaces is smaller in xeromorphic leaves than in mesomorphic ones. However, the ratio between the internal free surface area of the leaf and its external surface is small in shade leaves (6·8 to 9·9) and large (17·2 to 31·3) in xeromorphic leaves (Turrell, 1936). Similar results have been obtained by us from plants of various ecological types, e.g. in *Styrax officinalis*, which is a mesophyte, the ratio is 8·91, while in *Olea europaea* and *Quercus calliprinos*, which are xerophytes, it is 17·95 and 18·95 respectively. The increase in the free internal surface area is due to the increased development of the palisade tissue. The latter is probably one of the reasons why, besides the increase in photosynthetic activity, the rate of transpiration of xerophytes is high under conditions of favourable water supply.

In some xerophytes, and generally in halophytes, well developed water-storing tissues occur in the leaves. Water-storage tissue in the leaf consists of large cells with large vacuoles containing a dilute and/or mucilaginous cell sap. These cells have a thin layer of cytoplasm lining the cell walls in which scattered chloroplasts may be found. The osmotic pressure in the photosynthesizing cells is higher than in the non-photosynthesizing and when water is lacking they obtain their water from the water-storing tissue. As a result of this, the thin-walled water-storing cells shrink, but under favourable conditions of water supply they rapidly return to their former state (Schimper, 1898).

In the reduced leaves of *Salicornia*, broad and short tracheid-like cells are found among the palisade cells (Fahn and Arzee, 1959). The function of these cells has been variously interpreted by different workers. Duval-Jouve (1868) stated that they were filled with air. According to Holtermann

(1907) these cells transport water to the peripheral layers. Other investigators (Heinricher, 1885; Volkens, 1887; Solereder, 1908; De Fraine, 1912) believe that these tracheid-like cells have a water-storing function (Fig. 94). *Tracheoid idioblasts* may be scattered throughout the mesophyll as, for instance, in *Pogonophora schomburgkiana* of the Euphorbiaceae (Foster, 1956).

Involution of the leaves, which is especially typical of grasses, is a character of xerophytes. This feature is brought about by the action of bulliform cells and/or other epidermal and mesophyll elements which may be parenchymatous or sclerenchymatous (Shields, 1951).

There are plants, such as *Nerium oleander*, which, although growing in favourable wet conditions, have xeromorphic leaves, as these are defined today. On the other hand, plants, such as *Prunus amygdalus* and *Anagyris*, which grow in dry habitats, have leaves of mesomorphic character. However, in the majority of cases there is a correlation between all the abovementioned xeromorphic features, or some of them, and the dry conditions of the habitat. It is necessary to continue the investigation of additional anatomical and physiological features in order to understand better how desert plants withstand conditions of extreme drought.

STRUCTURAL CHANGES OF LEAVES OF WATER PLANTS (HYDROPHYTES)

In contrast with the different types of xerophytic habitats, water provides a uniform habitat and therefore the anatomical structure of water plants is less varied than that of the xerophytes. The factors that influence water plants are principally temperature, air and the concentration and composition of salts in the water. The most striking structural features in the leaves of water plants are the reduction of supporting and protective tissues, the decrease in the amount of vascular tissue, especially xylem, and the presence of air chambers.

The epidermis of water plants does not have a protective function and it plays a part in the uptake of nutrient substances from the water and in gas exchange. The cuticle is very thin, as are the cell walls. The epidermal cells of many hydrophytes contain chloroplasts. Immersed leaves are usually devoid of stomata although sometimes vestigial stomata may be found. Many stomata are, however, present on the upper surface of floating leaves.

In many species of water plants, e.g. *Ceratophyllum*, *Myriophyllum* and *Utricularia*, the leaves are divided into narrow cylindrical lobes which greatly increase the area of contact with the water. In *Ranunculus aquatilis* the floating leaves are entire, while the immersed leaves are divided into narrow lobes.

In the leaves and stems of hydrophytes *air chambers*, filled with gases, are found (Fig. 93, no. 3; Fig. 97, no. 1). These chambers are intercellular

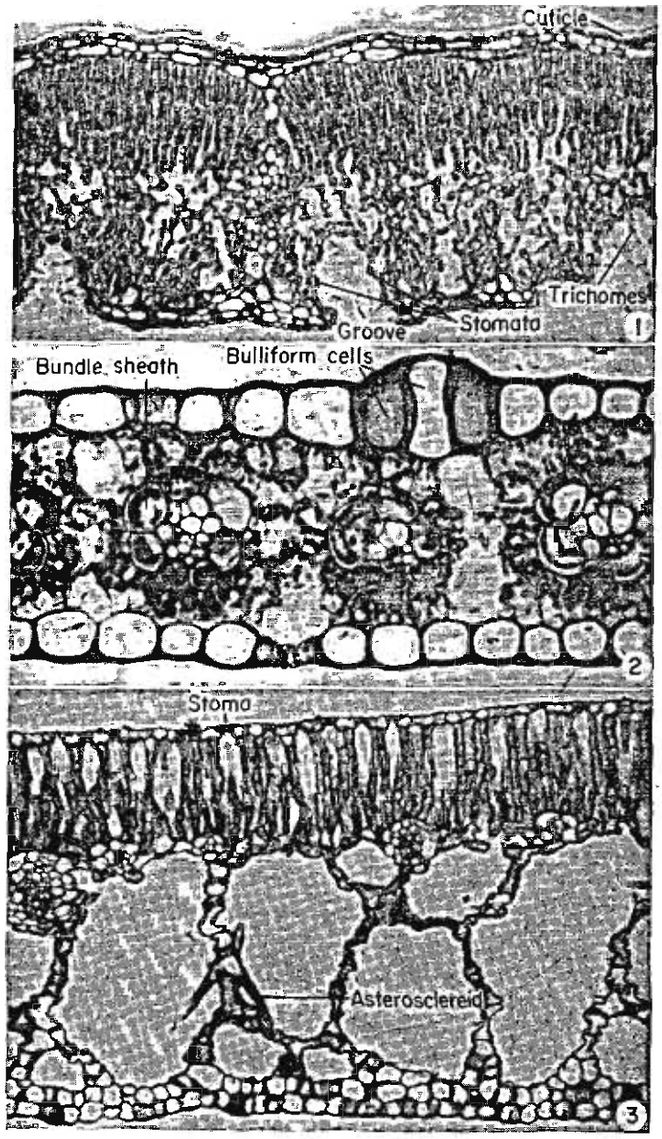

FIG. 93. Micrographs of portions of cross-sections of leaf laminae. 1, *Nerium oleander* showing the thick adaxial cuticle, multiseriate epidermis, dorsiventral arrangement of the mesophyll and the abaxial grooves in which the stomata are situated and in which there are many trichomes. ×95. 2, *Zea mays* showing a group of bulliform cells, the uniform structure of the mesophyll and the bundle

spaces which are usually regular in shape and which pass through the entire leaf. In many plants the air chambers may penetrate deep into the tissues of the stem. This type of structure can be seen in the leaves of *Potamogeton* and *Eichhornia*. The air chambers are usually separated from one another by thin partitions of one or two layers of chloroplast-containing cells. Cross partitions also occur in the air passages—elongated air cavities arranged parallel to the longitudinal axis of the organs—where they are termed *diaphragms* (Fig. 96, nos. 1, 2). The diaphragms consist of a single layer of cells with small intercellular spaces which appear as small pores and which apparently allow the passage of gases but not of water.

The most specialized tissue found in the stem and respiratory roots of many water plants is the *aerenchyma* (Fig. 95, no. 3). Aerenchyma is, strictly speaking, a phellem tissue derived from a typical phellogen of either cortical or epidermal origin (Haberlandt, 1918). During the development of this phellem single cells, at constant intervals from each cell layer, elongate in a radial direction (in relation to the organ) while the cells between them remain short. This lengthening of the cells pushes the previously formed layer of cells outwards so that numerous elongated air chambers, parallel to the axis of the plant, are formed. The elongated cells form the radial walls of the air chambers, while the non-elongated cells form the tangential walls. From the physiological point of view, however, any tissue that contains large intercellular spaces is termed aerenchyma.

Immersed hydrophytes contain very little sclerenchyma and may even be devoid of this tissue. Strips of sclerenchyma are, however, sometimes found along the leaf margins.

The root system of hydrophytes is usually very reduced and it principally provides an anchorage in the soil as the uptake of water and salts is carried out by the leaves and stems. For the same reason the vascular system is also much reduced. The reduction is especially obvious in the xylem tissue. In many species the xylem of the large veins is represented by only a few elements and in many of the small veins tracheary elements are completely absent. In such plants a duct similar to an air passage is present in the position of the xylem. The phloem is also reduced in comparison with that of land plants, but not to the same extent as is the xylem.

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sheaths which consist of a single layer of thin-walled cells. ×210. 3, *Nymphaea alba* showing stomata in the adaxial epidermis, several layers of palisade cells with veins immediately below them and the wide region of tissue containing large air cavities, in the walls of which are asterosclereids. The abaxial epidermis is devoid of stomata. ×110.

STRUCTURE OF THE PETIOLE

A similarity exists between the tissues of the petiole and those of the stem. The epidermis of the petiole is continuous with that of the stem. The parenchyma cells of the petiole, like those of the cortex, contain only a few chloroplasts especially as compared with the cells of the lamina.

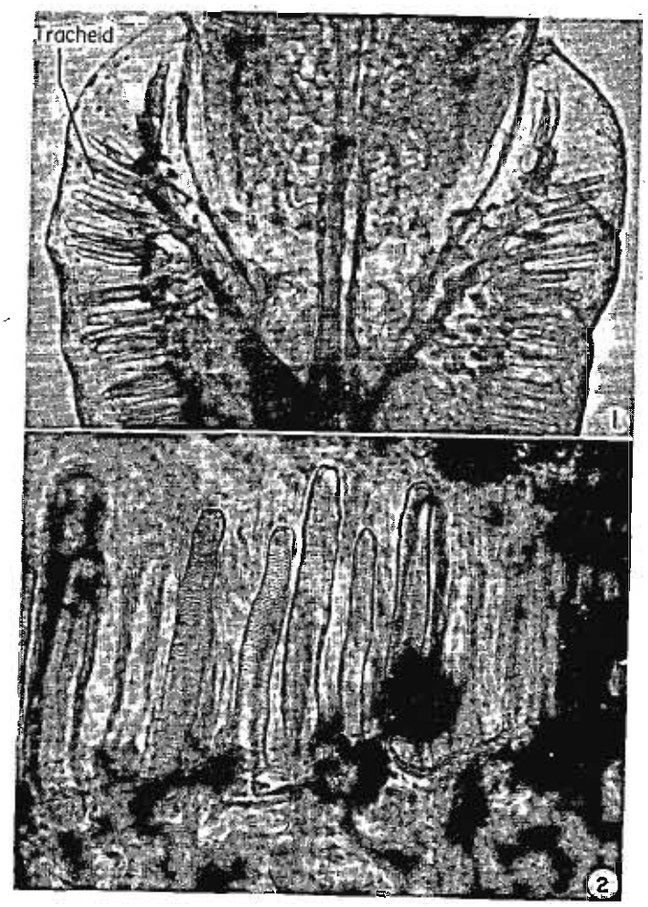

FIG. 94. 1, Micrograph of a node and reduced leaves of a cleared stem of *Salicornia*, showing the tracheids which are present in the region of the palisade parenchyma. These tracheids store water and they are connected to the vein endings present in the leaves and in the stem cortex. ×40. 2, Portion of above in region of tracheids, showing the helical thickening of the tracheids. ×120.

The supporting tissues of the petiole are collenchyma and/or sclerenchyma. The vascular bundles of the petiole may be collateral, e.g. *Ligustrum* (Fig. 98, no. 1), bicollateral, e.g. *Nerium*, or concentric, as in certain pteridophytes and many dicotyledons. The phloem is accompanied, in many species, by groups of fibres. The arrangement of the vascular tissues in the petiole differs in different plants. It may appear in a cross-section of the petiole as a continuous or an interrupted crescent, e.g. *Olea*, *Nicotiana*, *Nerium*, or as an entire or interrupted ring, e.g. *Ricinus*, *Quercus calliprinos*,

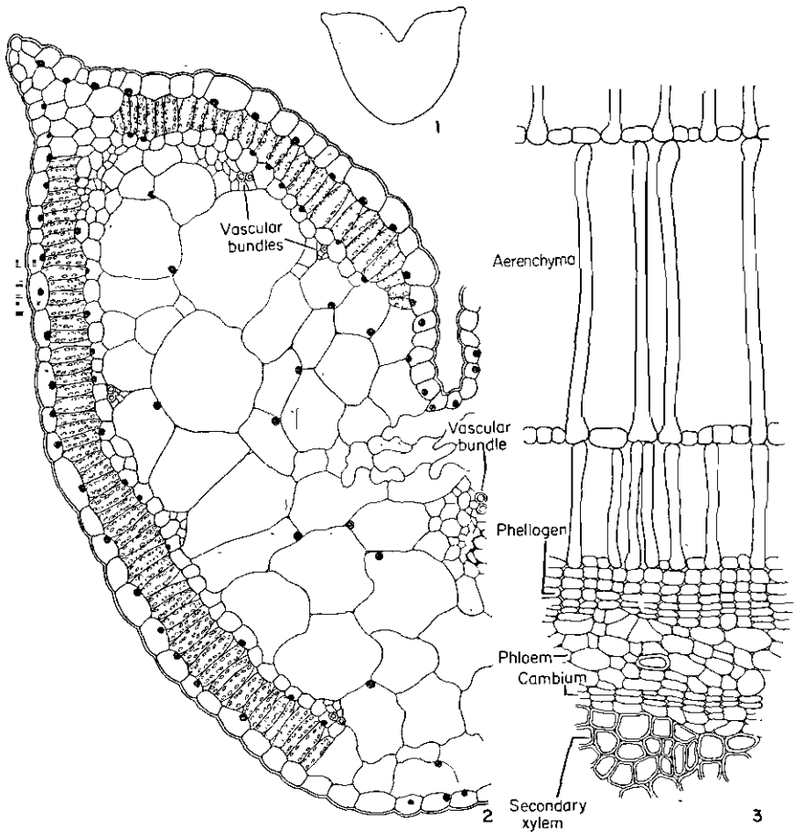

FIG. 95. 1 and 2, Succulent leaf of *Salsola kali*. 1, Outline of entire cross-section of lamina. 2, Detailed diagram of one half of the lamina showing palisade parenchyma on both sides of the leaf and the central portion of large, water-storing parenchyma cells. 3, Portion of a cross-section of an aerial pneumatophore of *Jussiaea peruviana* in which secondary vascular tissues, phellogen and aerenchyma can be distinguished. (Nos. 1 and 2, adapted from Shields, 1951; no. 3, adapted from Palladin, 1914.)

Q. boissieri (Fig. 98, no. 2), *Citrus* (Fig. 102, no. 1), or as a ring with additional internal and external bundles, e.g. *Vitis*, *Platanus*, *Robinia*, *Pelargonium*. An arrangement of scattered bundles is seen in many mono-

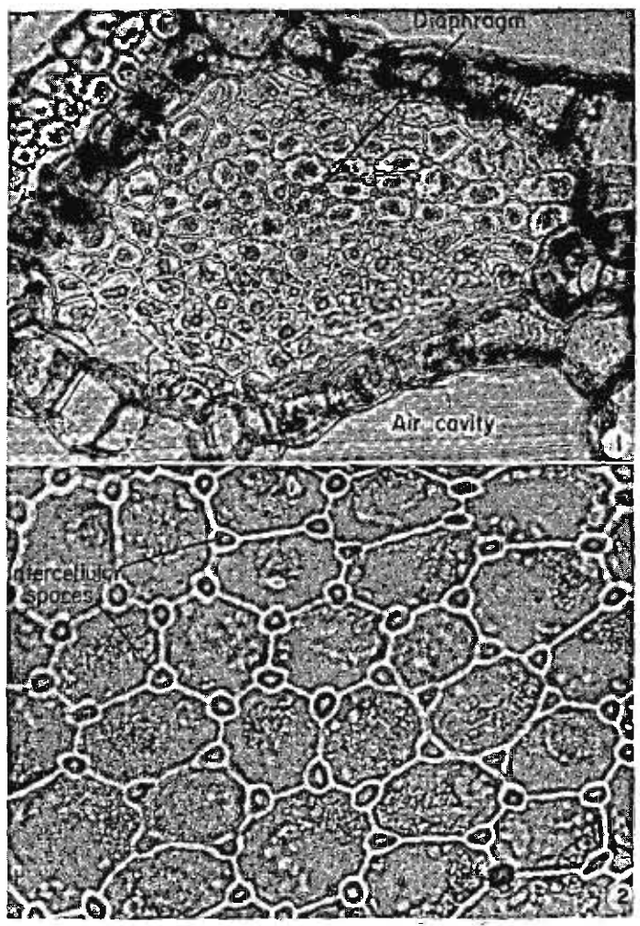

FIG. 96. 1, Micrograph of portion of a cross-section of the leaf of *Butomus* showing a diaphragm traversing an air passage. ×145. 2, Portion of the diaphragm enlarged. ×450.

cotyledons and in *Rumex*. If there is a single collateral bundle in the petiole, the phloem is found on the abaxial side and if the bundles are arranged in a ring the phloem is external to the xylem on the periphery of the ring.

In certain plants the base of the petiole appears swollen and contains a larger amount of parenchyma than the rest of the petiole. Such a petiole base is termed a *pulvinus*. In such cases where this area is capable of bringing about leaf movement, as in *Mimosa pudica*, for example, the parenchyma cells on the active side of the pulvinus have thinner walls. Intercellular spaces are present and there appears to be a close association between the cytoplasm and the cell wall.

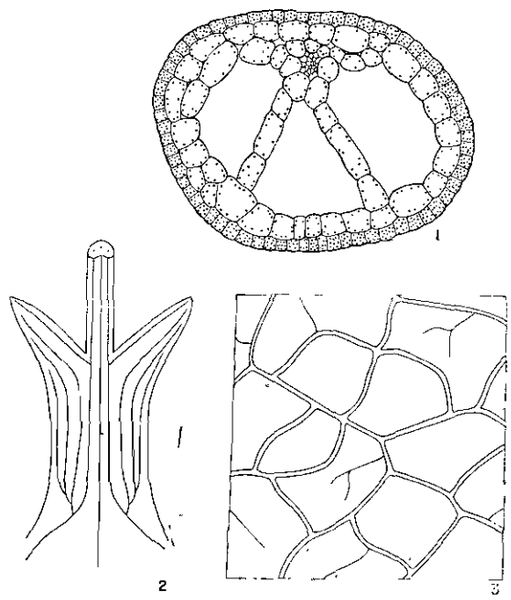

FIG. 97. 1, Cross-section of a leaf of *Ceratophyllum submersum*. 2, Diagram of the leaf base of *Trifolium* showing that the vascular supply of the stipules is derived from the lateral leaf-traces. 3, Surface view of the venation of a mature portion of the leaf of *Quercus calliprinos;* the veins that are accompanied by bundle-sheath extensions are represented by double lines and those without such extensions by a single line. (No. 1, adapted from Troll, 1948; no. 2, adapted from Foster and Gifford, 1959.)

VASCULAR SYSTEM OF THE LEAF

As has already been noted in the chapter on the stem, one, two, three or many leaf traces enter the leaf. The leaf traces may continue in the same number throughout the entire length of the leaf or they may divide, fuse and branch again later. Single or several closely associated vascular bundles form the *veins*. The term vein is sometimes used to include the vascular tissue together with the non-vascular tissue that surrounds it.

There are plants, such as certain species of the Coniferales and *Equisetum*, in which the leaf has but a single vein. However, in most of the higher pteridophytes and the majority of the angiosperms the leaf contains numerous veins. The arrangement of the veins in the leaf is termed *venation.*

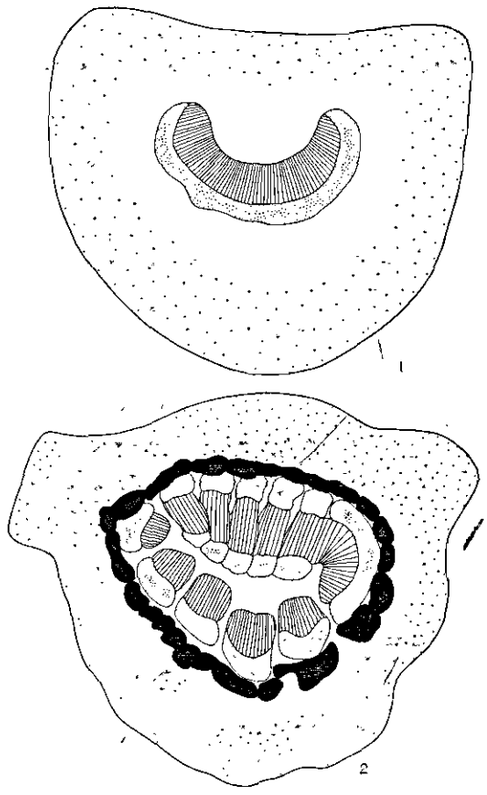

FIG. 98. Cross-sections of petioles. 1, *Ligustrum japonicum* in which the bundle is crescent-shaped. 2, *Quercus boissieri* in which the bundles are arranged in a ring. White areas—parenchyma; sparsely stippled areas—collenchyma; densely stippled areas—phloem; hatched areas—xylem; solid black areas—sclerenchyma.

In the angiosperms two main types of venation are usually distinguished —reticulate and parallel venation. In leaves with reticulate venation, which is the commonest type among the dicotyledons, the veins are of different sizes depending on the degree of branching. As a result of branching and fusing a network of veins is formed. In leaves with parallel venation, which is the commonest type among the monocotyledons, the main veins continue throughout the entire leaf and are almost parallel for most

of their length but approach one another and fuse at the leaf tip or both at the leaf tip and base. These "parallel" veins are interconnected by very thin bundles which are scattered throughout the lamina (Fig. 99, no. 2). In certain monocotyledons, e.g. *Zantedeschia*, a special type of venation is found. Here the veins are parallel for a certain distance, after which they spread out in a feather-like pattern. In these leaves there are also small veins that connect the main veins. Parallel venation can also be found in certain dicotyledons, e.g. *Plantago*, *Geropogon* and *Tragopogon*, and reticulate venation also occurs in certain monocotyledons, e.g. genera of the Orchidaceae, in *Smilax* and *Arum*.

When the venation is reticulate the largest vein passes through the median part of the leaf and it forms the main or central vein from which smaller veins branch. In certain leaves numerous large veins can be seen spreading out, as rays, from the base of the leaf lamina toward its margins. Those parts of the lamina through which the larger veins, both main and secondary, pass are usually thicker and project as ribs on the abaxial side of the leaf. These ribs are formed of parenchymatous tissue which is poor in chloroplasts, and of supporting tissue which is usually collenchyma. Therefore the larger veins have no direct contact with the mesophyll, in the narrow sense of the word. The small veins that form a network between the larger veins, and which occur in the mesophyll proper, are usually situated in the outermost layer of the spongy mesophyll which borders the palisade cells (Fig. 88, nos. 2, 3; Fig. 92, no. 1; Fig. 93, nos. 1, 3).

The small veins usually form networks. These networks vary in size and shape, and they accordingly subdivide the area of the mesophyll. The smallest areas, which are bounded by the thinnest branches of the bundles, are called *areoli*, and they usually contain terminal vein-endings which end blindly in the mesophyll (Fig. 99, no. 3). The degree of branching of these vein-endings differs in the leaves of different plants. Thus, for instance, in the leaves of *Euphorbia* (Fig. 99, no. 3) or *Ricinus*, very many such blind ends may be found in a single areole, in *Morus* there are somewhat fewer, in *Quercus boissieri* very few, and in the leaves of *Q. calliprinos* (Fig. 97, no. 3) blind vein-endings are absent or almost so.

In monocotyledons with parallel venation, the veins that pass along the entire leaf may be almost of the same thickness or they may be of different thicknesses. In the latter case the thick and thinner veins are arranged alternately. The median vein is usually the thickest.

In *Ginkgo* and many pteridophytes the veins do not form a closed system since the adjacent branches do not anastomose (Arnott, 1959). In such leaves all the terminal branches terminate freely within the lamina or along its margins. In many leaves of this type the branching of the veins is dichotomous.

In most cases the arrangement of the vascular tissue in the main vein resembles that in the petiole.

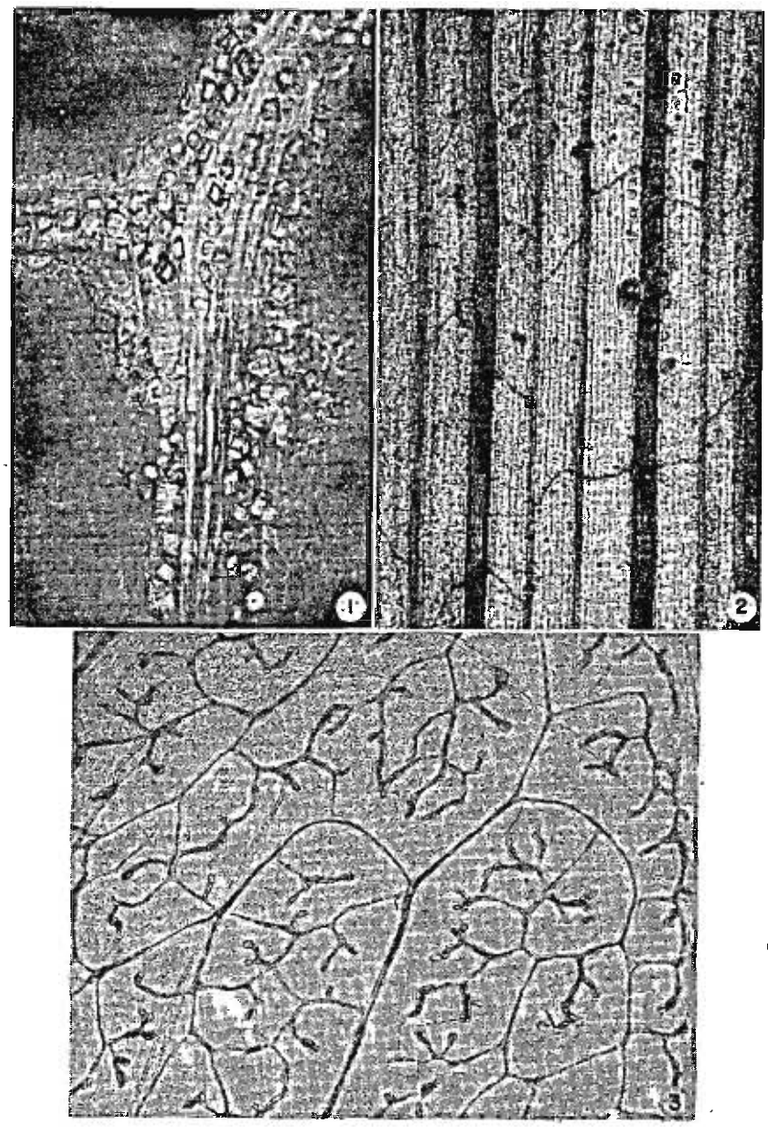

FIG. 99. Portions of cleared leaves as seen in surface view. 1, *Pistacia palaestina*, micrograph in polarized light in which the crystals in the cells of the bundle-sheath extensions can be seen. 2, *Lolium rigidum* showing minute veins which run transversely to the longitudinal axis of the leaf and which connect the parallel veins. ×35. 3, *Euphorbia milii* showing areoli with numerous blind vein endings. ×45.

The large veins in dicotyledonous leaves may consist of both primary and secondary tissues, while the smaller veins consist of primary tissues only. The large and medium-sized veins contain vessels and sieve tubes. In the smallest veins the tracheary elements are tracheids with annular and spiral wall thickenings. The phloem close to the vein-endings consists of parenchyma only. In dicotyledons the vein-endings often contain only tracheids, which may be single or in pairs or in irregular groups. Sometimes terminal sclereids may be found as a continuation of the tracheids (Foster, 1956; Fahn and Arzee, 1959) as, for instance, in *Mouriria*, *Boronia* and *Arthrocnemum glaucum* (Fig. 40, no. 2). The thin veins that connect the parallel veins of grass leaves may contain a single row of tracheary elements and a single row of sieve elements.

Much importance is given to the problem of the density of the veins in the leaf. The total length of the veins in a unit area of the leaf is usually great. Thus, for instance, we have found in *Quercus calliprinos* that the total length of the veins in a square millimetre is 11 mm and in *Q. boissieri*, about 14 mm. According to Wylie (1939, 1946) the average distance between the veins of the dicotyledonous leaf is about 0·13 mm.

As has already been mentioned, the leaf contains tissues in which the cells have many lateral connections (i.e. the epidermis and the spongy parenchyma) and others in which the cells have few lateral connections (i.e. the palisade parenchyma). Wylie also came to the conclusion that a correlation exists between the density of the veins and the volume of the mesophyll tissues. On the one hand, with increase in the volume of the palisade tissue, in which the conductivity in the direction parallel to the leaf surface is low, the distance between the veins becomes smaller and, on the other hand, with increase in the volume of the spongy tissue, in which conduction is efficient in the above-mentioned direction, the distance between the veins becomes larger.

Bundle sheaths

The large veins are surrounded by much parenchyma which is poor in chloroplasts. The smaller veins, also, are usually surrounded by a layer of tightly packed parenchyma cells; such a layer is termed the *bundle sheath*. In dicotyledons the cells of the bundle sheath are usually elongated in a direction parallel to the vein, but sometimes, as, for example, in *Atriplex halimus*, the cells are more or less cubical (Fig. 100, no. 2; Fig. 90, no. 2). The cells of the bundle sheath are thin-walled, and they may contain as many chloroplasts as the mesophyll cells, or they may contain only a few chloroplasts, or they may be devoid of them. Sometimes crystals may occur in the bundle-sheath cells (Fig. 99, no. 1). The bundle sheaths also surround the vein-endings. Although in most of the dicotyledons the

bundle sheath consists of parenchyma cells, there are some families, such as the Winteraceae (Bailey and Nast, 1944), in which the sheath is sclerenchymatous.

FIG. 100. 1, Micrograph of portion of a cross-section of the leaf blade of *Styrax officinalis* in which stellate hairs on the abaxial surface and bundle-sheath extensions can be distinguished. × 150. 2, Surface view of cleared leaf of *Atriplex halimus* in which the bundle sheaths surrounding the veins can be seen.

In many dicotyledonous leaves, such as those of *Styrax officinalis* and *Quercus,* among others, the parenchyma of the bundle sheath extends to the epidermis on one side or on both sides of the leaf. These plates of parenchyma cells usually reach the epidermis itself, and they are termed *bundle-sheath extensions* (Fig. 100, no. 1). There are proofs that the bundle-

sheath extensions have a conducting function in the leaf (Wylie, 1943, 1947, 1949, 1951). They conduct from the bundles to the epidermal cells, which are very closely connected laterally and which therefore function to conduct in a plane parallel to the leaf surface. In some plants the bundle-sheath extensions accompany the veins throughout almost their entire length, while there are other plants in which bundle-sheath extensions are

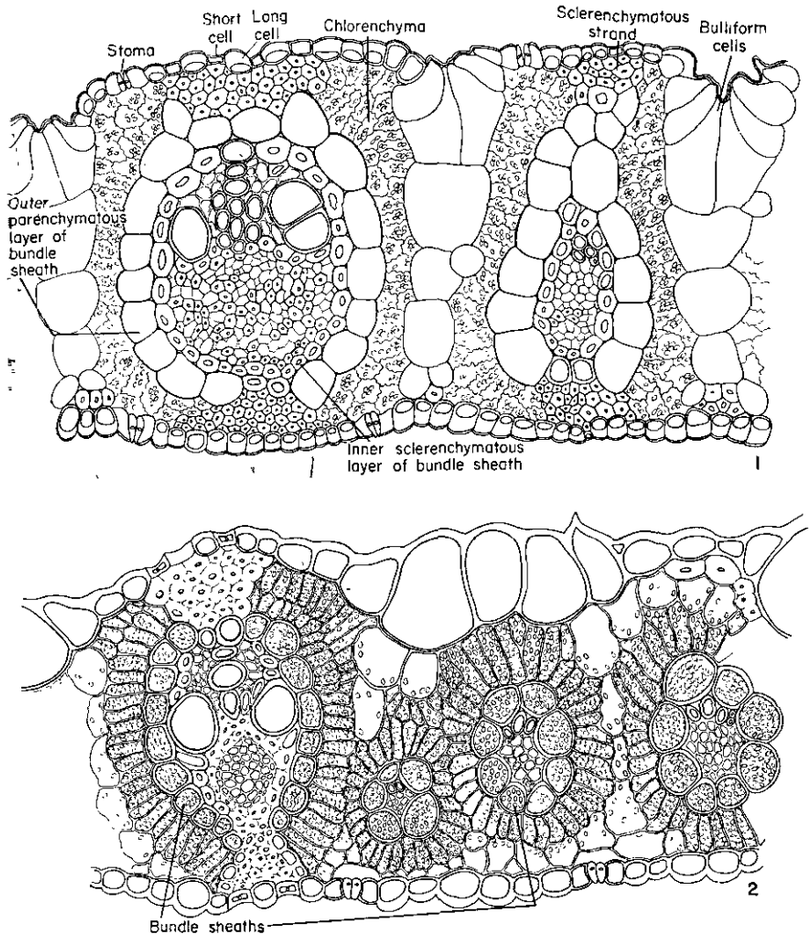

FIG. 101. Portions of cross-sections of grass leaves. 1, *Desmostachya bipinnata* in which the bundle sheath consists of two layers, the outer parenchymatous and the inner sclerenchymatous. ×260. 2, *Hyparrhenia hirta*, in which the bundle sheath consists of a single layer of chloroplast-containing cells. ×260.

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completely absent *(Olea, Pistacia lentiscus)*. In *Quercus calliprinos* 94% of the total vein length is accompanied by bundle-sheath extensions; in *Q. boissieri*, 71%; in *Styrax officinalis*, 62%; and in *Pistacia palaestina*, 50%. According to Wylie, the density of the veins in mesomorphic leaves is indirectly proportional to the total length of the bundle-sheath extensions.

Bundle sheaths also occur in the monocotyledons, especially in the grasses in which two types are distinguished. In the subfamily Panicoideae (with the exception of certain species of *Panicum*) the sheath consists of a single layer of thin-walled cells which contain chloroplasts (Fig. 101, no. 2). In the subfamily Pooideae the sheath consists of two layers of cells. The inner layer, which apparently develops from the procambium, consists of living, thick-walled, chloroplast-free cells which are elongated parallel to the veins, while the cells of the outer layer are thin-walled and mostly contain chloroplasts (Fig. 101, no. 1). On the small veins the inner layer may be present only on the side of the phloem.

The bundle sheath can be regarded as an endodermis. The contents and walls of the bundle-sheath cells often stain similarly to those of the endodermis and, in the young leaves of certain grasses and sedges, Casparian strips even have been observed in the walls of those bundle-sheath cells that are thick-walled when mature (Guttenberg, 1943; Van Fleet, 1950).

The parenchyma cells of the sheath may sometimes store starch, and then a "starch sheath" is formed.

Supporting tissues of the leaf

The epidermis, itself, because of its compact structure and the strength of the cuticle, and the fact that the walls of its cells may sometimes be thick or impregnated with silica, gives support to the lamina. Collenchyma is usually found close to the larger veins immediately below the epidermis and also on the leaf margins in dicotyledonous leaves. The bundle-sheath extensions may also be collenchymatous. In addition to collenchyma, sclereids are present in the mesophyll of many dicotyledons. The large and medium-sized veins in many plants, e.g. *Pistacia palaestina*, are accompanied by groups of fibres. In monocotyledonous leaves the vascular bundles are accompanied by many fibres. In the Gramineae and in many other monocotyledons the fibres form girders on one or both sides of the bundles, and in many leaves they continue from the bundle sheaths to the epidermis, the cells of which, in such regions, may then also become fibre-like (Fig. 101, nos. 1, 2).

SECRETORY STRUCTURES

Secretory structures, which participate in the secretion of water or other substances, are a common feature of leaves. Many of these secretory structures are of epidermal nature and are discussed in Chapter 10.

The substances produced may be excreted from the cells or they may be retained only to be released upon the disintegration of the cells.

Glands are present on many foliage leaves and cataphylls. These structures consist of a mass of dense parenchyma cells in which there terminates a vascular bundle. The parenchyma is covered by a glandular epidermis. The cells of such an epidermis are mostly elongated in a direction at right-angles to the surface of the gland (Fig. 68, no. 1) and have dense cytoplasm and large nuclei. The presence of these glands on the petioles and on the teeth of the laminar margins, for instance, are of great taxonomic importance because of their constant position in the species, and even varieties, in which they occur. The glands on different organs or parts of an organ of the same species may secrete different substances. In *Prunus persica* and other related species, for example, the glands on the laminar teeth secrete a bitter resinous substance, while those on the petiole secrete nectar.

Nectariferous glands are found on the petioles of many plants, e.g. *Passiflora*, *Ricinus* and *Impatiens*. In *Vicia* nectariferous tissue is present in the central portion of the stipule where it is easily distinguished because of the anthocyanins present in its cells.

Another type of secretory structure is the essential oil cavity which occurs characteristically in the mesophyll of the leaves of plants, such as *Eucalyptus*, *Gossypium* and *Citrus*, for example. These are examples of lysigenous cavities in which the secretions formed in the cells are released after the disintegration of the cells, the lysis of which forms the cavity (Fig. 88, no. 1).

Examples of other types of secretory structures found in leaves are schizogenous resin ducts, which are characteristic of the Compositae, Anacardiaceae and Coniferales; laticifers as found in *Euphorbia;* mucilage cavities found in the Sterculiaceae, different species of the Malvaceae, Moraceae and other families.

In leaves, secretory substances may also be found in idioblasts. These secretory cells are classified according to the substances secreted, although cells that contain a mixture of different substances also exist. The secreting idioblasts, like other secretory structures, are of important taxonomic significance (Metcalfe and Chalk, 1950). For instance, the secretory cells of the Lauraceae, Simarubaceae and Onagraceae contain oils. Cells containing the enzyme myrosin are found in the Cruciferae, Capparidaceae, Resedaceae, Tropaeolaceae and Moringaceae. Cells with a resinous content are found in the Meliaceae and in many species of the Euphorbiaceae, Rutaceae and Rubiaceae. Tannin-containing cells are found in the Anacardia-

ceae (especially in *Pistacia palaestina* and *P. lentiscus*), Annonaceae, Crassulaceae (especially in *Sempervivum tectorum* and species of *Echeveria*), Ericaceae, Euphorbiaceae, Buxaceae, Polygonaceae, Rosaceae, Tamarica-

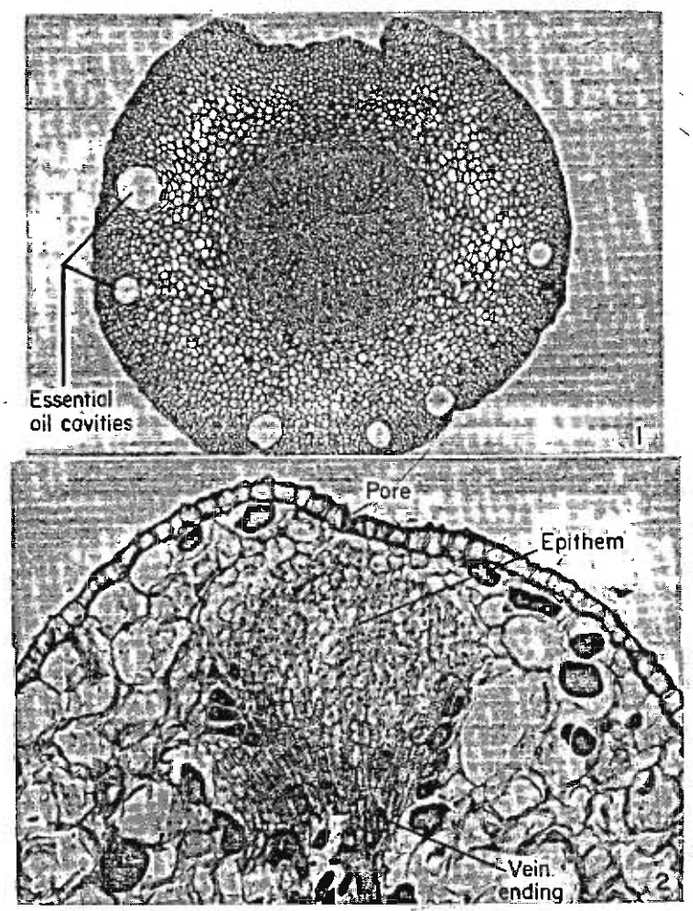

FIG. 102. 1, Cross-section of the petiole of *Citrus*; stem-like arrangement of vascular tissues and essential oil cavities can be distinguished. ×35. 2, Portion of section cut parallel to the surface of the leaf of *Sedum* sp. showing the structure of a hydathode. ×140.

ceae and Leguminosae. Cells with tannin compounds are also found in parenchyma of fruits, e.g. of *Ceratonia*. Cells with mucilaginous contents are found in the Buxaceae, many species of the Malvaceae, Chenopodia-

ceae and Rubiaceae, and in many monocotyledonous plants. Cells containing secretory substances that have not been identified are found in very many families, such as the Anacardiaceae, Fagaceae, Buxaceae, Aristolochiaceae, Cruciferae, Platanaceae, Plumbaginaceae, Rutaceae and Punicaceae.

Idioblasts with differing types of crystals and cystoliths are found in the leaves of different species as has already been described in previous chapters.

Special secretory structures are the *hydathodes* (Fig. 102, no. 2) which secrete water in the form of drops from within the leaf. This phenomenon is called *guttation*. Hydathodes secrete water which is brought to the surface by the terminal tracheids of the veins. This water passes through the intercellular spaces of the loosely packed parenchyma of the hydathode which is devoid of chloroplasts and which is called the *epithem*. The intercellular spaces open to the exterior by special pores which are of stomatal origin and which remain permanently open (Stevens, 1956). The epithem may be bounded by suberized cells or cells with Casparian strips. Some hydathodes lack a typical epithem. Haberlandt (1918) distinguished two different types of hydathode—*active hydathodes* and *passive hydathodes*. Both these types are more broadly discussed by Sperlich (1939). In the opinion of certain workers the term hydathode should be used only for those organs through which water is secreted passively (Stocking, 1956). According to them the active hydathodes of Haberlandt might better be considered as glands that secrete dilute nectar. Typical hydathodes occur on the leaves of *Brassica* and plants belonging to the Crassulaceae among others.

HISTOLOGY OF THE GYMNOSPERM LEAF

Most gymnosperms are evergreen and their leaves are usually xeromorphic. Two types of gymnosperm leaf will be described here—that of *Cycas* and that of conifers, such as *Pinus* and *Cedrus*.

The leaf of *Cycas* (Fig. 103, no. 1) is leathery and stiff, the epidermal cells are thick walled and have a thick cuticle, and the stomata are sunken and occur on the abaxial surface of the leaf. The mesophyll consists of palisade and spongy parenchyma as in angiosperms. A uni- or biseriate hypodermis is present between the adaxial epidermis and the palisade parenchyma. The xylem of the median vein is of a special primitive type. The protoxylem is present on the abaxial side and the metaxylem on the adaxial side. The protoxylem is accompanied by a small amount of parenchyma. Secondary xylem develops near the phloem from a cambium situated between the two types of vascular tissue. The vein is surrounded by an endodermis. The *transfusion tissue*, which consists of tracheids and elongated parenchyma cells, occurs on both sides of the vein. This tissue is cha-

racteristic of the gymnosperms and it is assumed that it plays a part in the passage of water and nutrient substances between the bundle and the mesophyll.

The epidermis of the needle-like leaves of *Pinus* (Fig. 103, no. 2) and *Cedrus* (Fig. 104, nos. 1, 2) consists of extremely thick-walled cells and is cov-

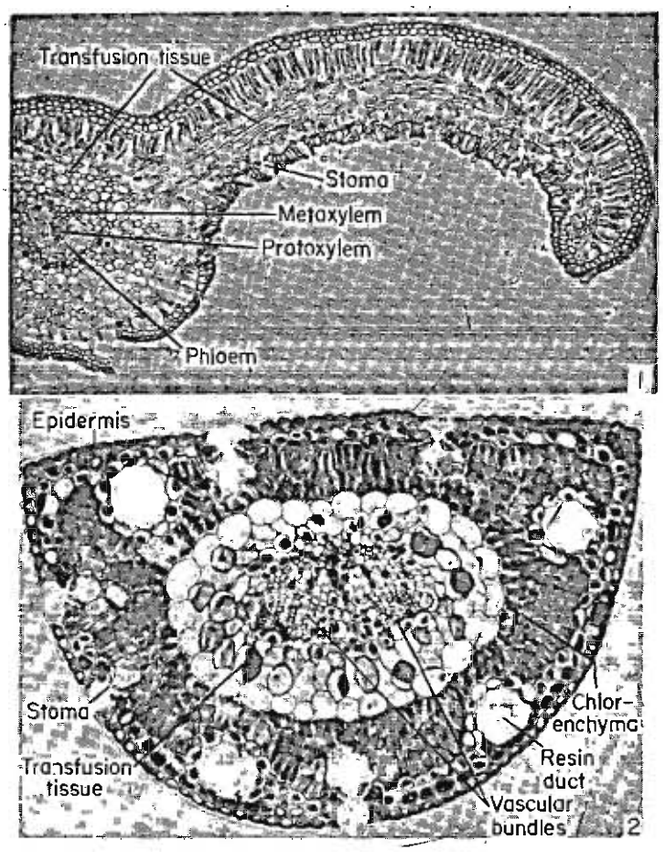

FIG. 103. Micrographs of cross-sections of gymnosperm leaves. 1, A leaflet of *Cycas revoluta*. ×35. 2, *Pinus halepensis*. ×110.

ered with a thick cuticle. The stomata are scattered on all sides of the leaf; they are sunken and are overarched by the subsidiary cells (Fig. 103, no. 2). A hypodermis of fibre-like cells is present except in the areas below the stomata. The mesophyll is of a parenchymatous nature. The walls of the mesophyll cells have characteristic ridge-like invaginations into the cells.

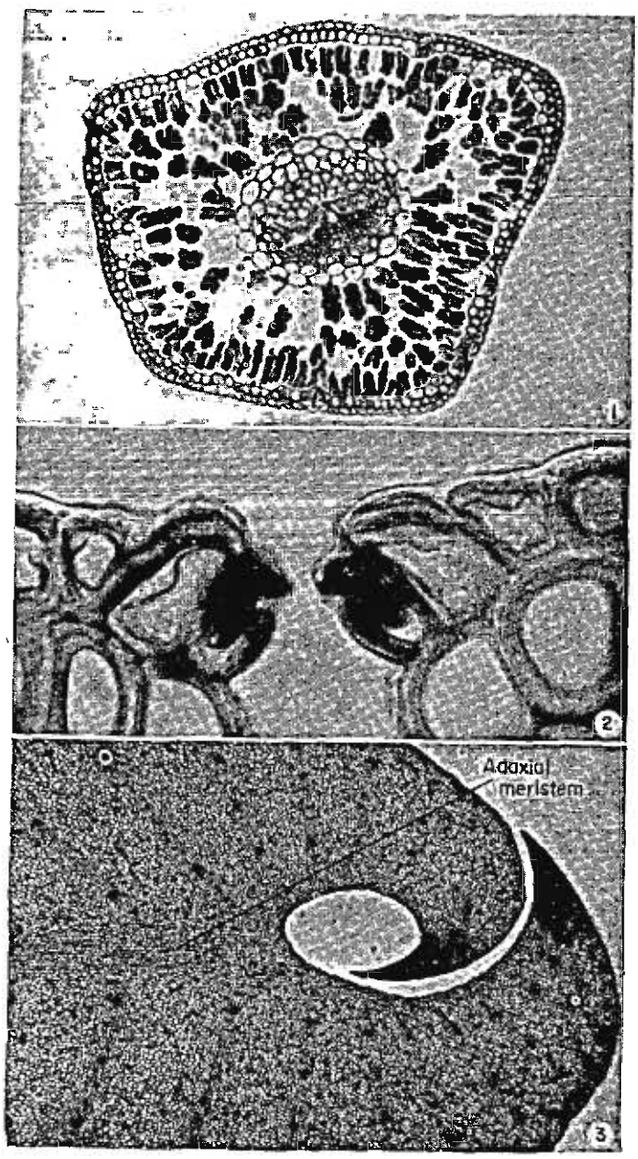

FIG. 104. 1, Micrograph of a cross-section of the leaf of *Cedrus deodara*. ×40. 2, Cross-section of a stoma of *C. deodara*. ×430. 3, Portion of a cross-section of a developing leaf of *Musa* showing the adaxial meristem. ×40.

These cells contain chloroplasts. Resin ducts are also present in the mesophyll. In the centre of the leaf there is a single vascular bundle, or two, which are then close to one another. The arrangement of the proto- and metaxylem is as in angiosperms, i.e. the protoxylem is on the adaxial side and the metaxylem on the abaxial side close to the phloem. The bundle is surrounded by transfusion tissue consisting of tracheids and of living parenchyma cells. The parenchyma cells contain tannins, resins, and also starch in certain seasons of the year. The tracheids closest to the bundles are long while those further away are more parenchyma-like and have relatively thin, slightly lignified walls and bordered pits. Because of their thinner walls these tracheids are not able tc withstand the pressure of the living cells around them in which the turgor is higher, so they become somewhat crushed. In the transfusion tissue close to the phloem there are certain cells that have dense cytoplasm and which are similar to albuminous cells. The vascular bundles together with the transfusion tissue are surrounded by a sheath of relatively thick-walled cells—the endodermis (Fig. 103, no. 2; Fig. 104, no. 1).

Development of the foliage leaf

The development of the leaf can be divided, although artificially, into the following stages; initiation, early differentiation, development of the leaf axis, origin of the lamina. histogenesis of the tissues of the lamina.

INITIATION

The initiation of the leaf commences with periclinal divisions in a small group of cells on the sides of the apex. The number of cell layers, however, that begin to divide thus and their position on the apex varies considerably in different plants. For example, in many grasses, it was found that leaf initiation starts with periclinal division in the cells of the surface layer of the apex (i.e. in the outermost layer of the tunica) and in cells of the layer immediately below it (Sharman, 1942, 1945; Thielke, 1951). In this case the main portion of the leaf primordium originates from the outermost cell layer of the shoot apex.

Contrary to the situation in the grasses, in other monocotyledons, e.g. *Tulipa* (Sass, 1944), and apparently in all the dicotyledons thus far examined, the first periclinal divisions do not take place in the cells of the surface layer, but in the cells of one or more layers below it. In the apices of such plants, therefore, the surface layer does not take part in the initiation of the inner tissues of the leaf. This layer enlarges by numerous anticlinal divisions of its cells and so becomes adapted to the growth of the primordium. The surface layer gives rise to the protoderm of the young leaf.

In the gymnosperms there is the same amount of variation in the initiation of the leaf primordia as there is in the angiosperms. In *Taxodium distichum*, for example, the initiation of the leaf primordium originates with periclinal divisions in the cell layer immediately below the surface layer of the apex (Cross, 1940), while in most of the Coniferales and in *Zamia* (Korody, 1937; Johnson, 1943) the periclinal divisions take place in the surface layer of the apex as well as in the layer below it.

Most commonly the initiation of the leaf primordium commences in cell layers below the surface layer. In this case the degree to which the inner cell layers of the tunica and the neighbouring cell layers of the corpus participate in the initiation of the primordium differs, and it is difficult to determine accurately the part played by each of them. In order to clarify this problem periclinal cytochimeras, produced by the application of colchicine, have been used. With the aid of such cytochimeras it has been possible to show from which layers of the apex the various tissues of the leaf develop (Satina and Blakeslee, 1941; Dermen, 1947, 1951). Dermen thus was able to determine that in *Vaccinium* and *Pyrus malus*, for instance, three cell layers of the apical meristem take part in the formation of the leaf. The leaf epidermis develops from the outermost layer (i.e. from the outer tunica layer) by anticlinal divisions. The second and third layers (i.e. the inner layer of the tunica and the outermost layer of the corpus) give rise to the mesophyll and the vascular bundles.

EARLY DIFFERENTIATION

As a result of continued cell division the leaf primordium protrudes from the shoot apex as a buttress which has the form of a small papilla or crescent. This leaf buttress consists of a protoderm layer, an inner mass of ground meristem and a procambial strand which develops acropetally from the nearby procambium of the stem (see Chapter 11).

DEVELOPMENT OF THE LEAF AXIS

In many dicotyledons and gymnosperms the development of the leaf axis precedes that of the lamina or of the leaflets (in a compound leaf).

As a result of the rapid development the primordium becomes shaped like a gradually tapering cone the adaxial side of which is flattened (Fig. 105, no. 1). The tip of the cone functions for a while as an apical meristem, but in spermatophytes the cells at the tip of the leaf exhibit histological signs of maturation relatively soon. In certain plants, from that early stage of development when the primordium is still less than 1 mm long, all further increase in length is due to the division and elongation of cells

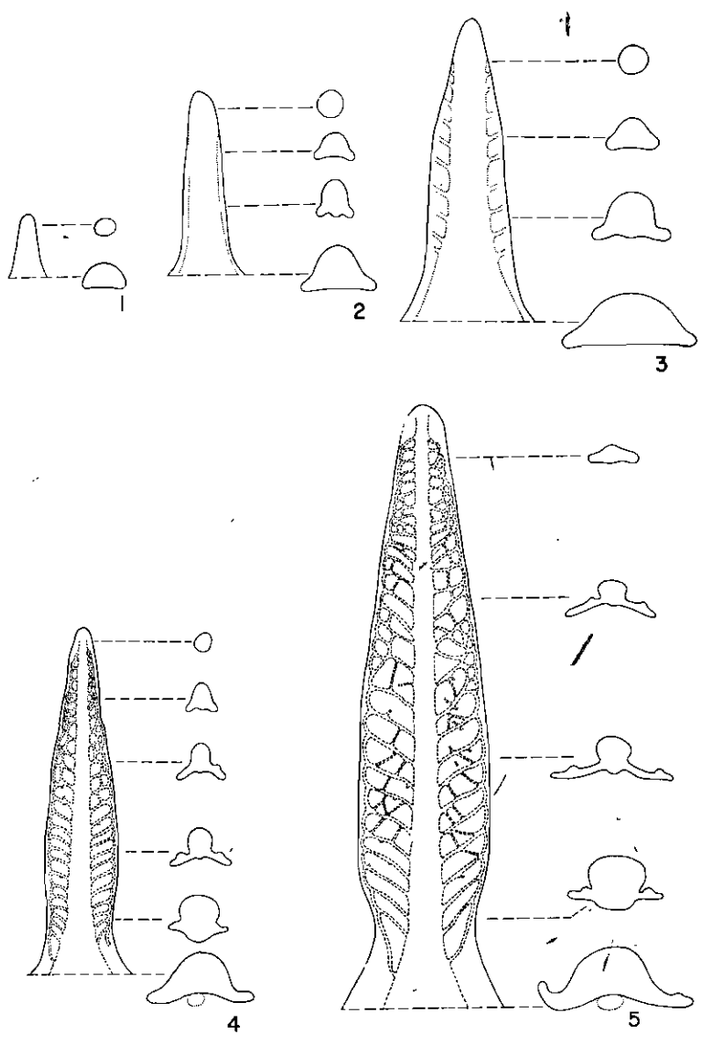

FIG. 105. Diagrams of longitudinal and cross-sections of leaf primordia of *Nicotiana tabacum* at different ontogentic stages. 1, A young, more or less cone-shaped primordium. 2, Primordium in which the narrow margins, from which the lamina will develop, can be seen. 3, Primordium in which the beginning of development of the main lateral veins can be seen. 4, Primordium 5 mm long in which the early development of the provascular system can be seen. 5, A more advanced stage. Nos. 1–3, ×25; nos. 4 and 5, ×10. (Adapted from Avery, 1933.)

distant from the tip of the primordium, i.e. by intercalary growth. In leaves of ferns, however, the apical growth continues for a long period together with the addition of cells by intercalary growth in an acropetal direction. The increase in length of the axis is usually accompanied by an obvious increase in width. This thickening is particularly striking in those numerous plants in which a cambium-like region, in which the cells divide tangentially, develops along the adaxial side of the primordium. This cambium-like region is termed the *adaxial meristem* or *ventral meristem* (Fig. 104, no. 3) and from it *accessory bundles* may develop (Foster, 1936, 1950; Kaufman, 1959).

ORIGIN OF THE LAMINA

During the preceding elongation and thickening of the axis of the young leaf, the cells of the adaxial margins continue to divide very frequently—much more so than the inner cells of the ground meristem. In simple leaves two wing-like strips (Fig. 105, nos. 2, 3) usually develop on the margins as a result of the accelerated growth of these cells. In leaves with a petiole the marginal growth is depressed in the basal portion of the leaf axis which then develops into the petiole. In a cross-section both sides of the developing lamina can be seen to consist of protoderm enclosing a few layers of ground tissue. The new cells that are added to the different layers of the lamina originate from rows of *marginal initials* and *submarginal initials* (Fig. 106, nos. 1–2).

The marginal initials are the cells of the outermost layer on the margins of the young lamina. Generally, in the angiosperms these initials divide only anticlinally and so add new cells to the abaxial and adaxial protoderm. In certain monocotyledons and in the bud scales of *Rhododendron* spp. periclinal divisions also occur, resulting in the addition of new cells to the nearby ground meristem (Foster, 1937; Sharman, 1942, 1945). In the variegated leaves of certain plants the white margins may develop as a result of periclinal divisions in the protoderm (Renner and Voss, 1942).

The submarginal initials undergo divisions in various planes. These cells give rise to new cells which are added to the inner layers of the young lamina.

In pinnately and palmately compound leaves the lateral leaflets develop from the adaxial marginal meristem of the axis of the young leaf as two rows of papillae. In certain plants the order of development of the leaflets is acropetal, e.g. *Carya* (Foster, 1932, 1935), but in many other plants the order is basipetal. As is seen in *Carya*, the primordium of each lateral leaflet first develops an axis and the laminae of the leaflets later develop from the margins of these axes. The tip of the main axis develops into a terminal leaflet.

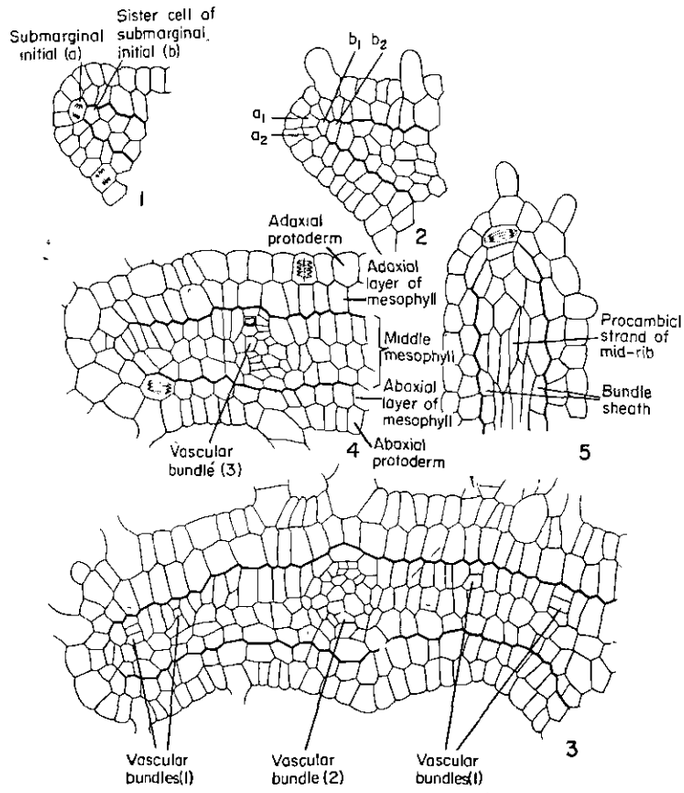

FIG. 106. 1–4, Cross-sections of the marginal portions of leaves of *Nicotiana tabacum*, at different stages of development, showing the divisions which, together with the enlargement of the cells, result in the growth of the young lamina. 1, Showing the direction of division in the protoderm and submarginal initial. The cell *b* is a sister cell of the submarginal initial (a) and both are derived from a periclinal division of a submarginal initial in that position. 2, Showing the two cells, a_1 and a_2 resulting from the anticlinal division of *a*, and the cells b_1 and b_2 which arose from the periclinal division of *b*. 3 and 4, Development of mesophyll and provascular strands; different stages of development of the vascular bundles are indicated by numerals. 5, Median longitudinal section of a primordium showing the provascular strand of the mid-rib. (Adapted from Avery, 1933.)

HISTOGENESIS OF THE TISSUES OF THE LAMINA

The marginal growth apparently continues longer than does the apical growth but it, too, ceases relatively early. In *Nicotiana tabacum*, for example, Avery (1933) observed that marginal growth continues, at least

in the lower part of the lamina, until that stage where the leaf is several centimetres long. In *Cercis siliquastrum* (Slade, 1957) marginal growth of the lamina is completed by the time the leaf measures 2–2·5 mm. In the leaf of the Dwarf Cavendish banana, in which a marginal vein is differentiated in the early stages of development of the leaf primordium, mar-

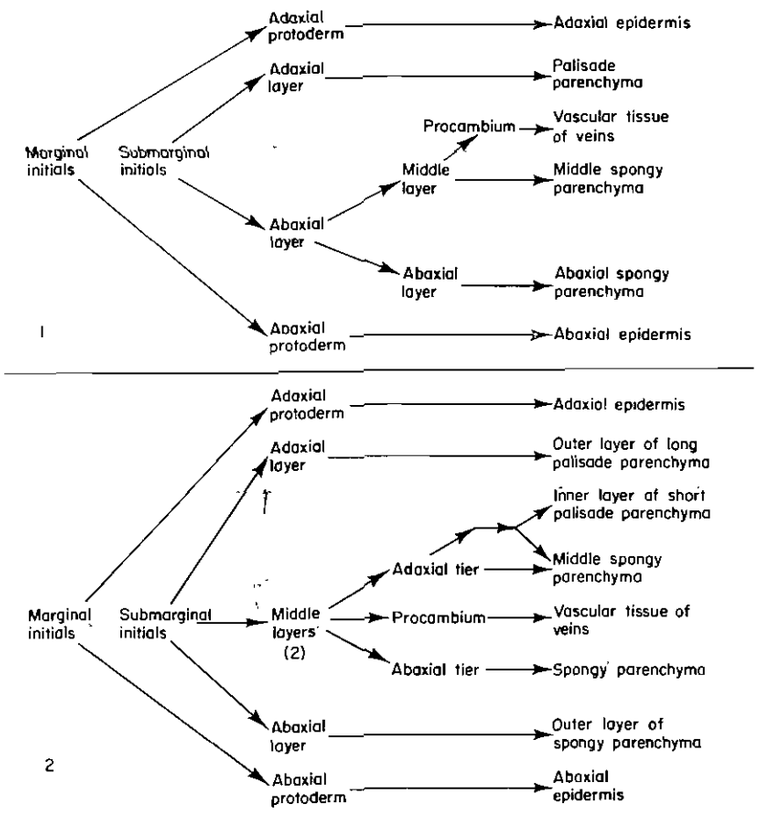

FIG. 107. Diagrammatic representation of leaf histogenesis. 1, *Carya buckleyi*. 2, *Pelargonium zonale*. (Adapted from Foster, 1936.)

ginal growth in the laminar part of the primordium ceases as early as between the fourth and sixth plastochron. Marginal growth on the right side of the mid-rib ceases in the fourth plastochron when the primordium is about 5 mm long whereas, on the left side, it ceases during the sixth plastochron when the primordium is about 20 mm long. After the cessation of marginal growth, further growth of the lamina is brought about by cell division in the various cell layers of the lamina. These divisions

are mostly anticlinal and thus a *plate meristem* (Fig. 106, nos. 3, 4) is formed. A plate meristem is one in which the planes of cell divisions in each layer are perpendicular to the surface of the organ in which the meristem occurs. The activity of such a meristem results in increase in surface area but not in thickness of the organ. In the lamina the cells of this meristem have a stratified arrangement and therefore it is possible to

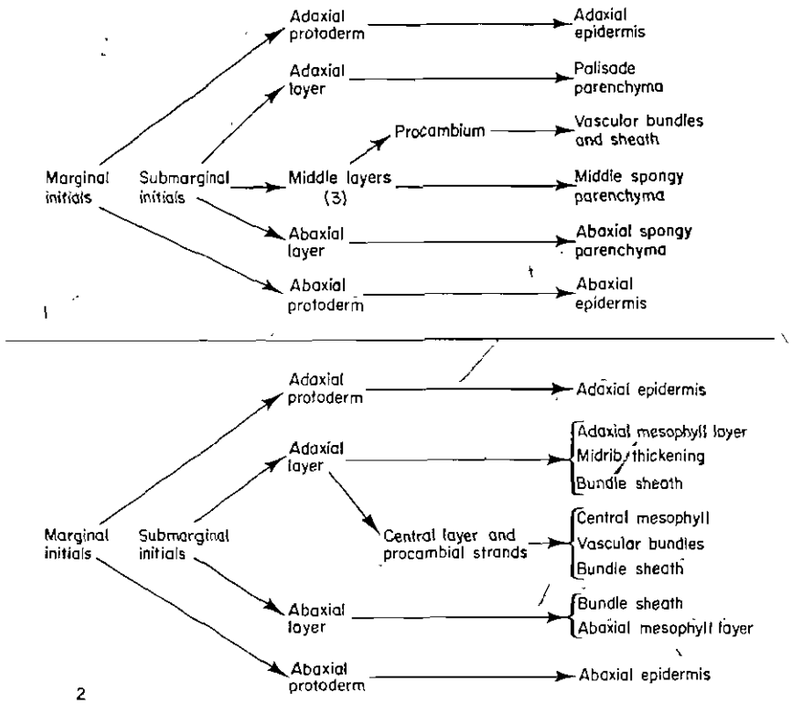

FIG. 108. Diagrammatic representation of leaf histogenesis. 1, *Nicotiana tabacum.* 2, *Oryza.* (No. 1, adapted from Foster, 1936; no. 2, adapted from Kaufman, 1959.)

trace, with relative ease, the origin of the epidermis, palisade and spongy tissues, and the vascular bundles. In Fig. 107 and 108, it can be seen how, in different plants, these tissues develop from the cell layers of the young lamina.

The regular arrangement of the cell layers is interrupted to differing extents by the development of the vascular bundles, their sheaths and supporting tissues. As a result of this, in the final stages of the expansion of the leaf surface the regular arrangement of the cell layers becomes

restricted to those areas of the lamina between the large lateral veins. The palisade parenchyma is one of the last tissues to cease growing and dividing. This tissue may continue to function as a meristem for some time after the cells of the spongy parenchyma and of the epidermis have ceased to divide.

The different parts of the leaf expand at different rates and in different directions (Avery, 1933). This type of growth has been termed anisotropic growth (Ashby, 1948a). The type of growth of a leaf is controlled by genetic factors, but it is also influenced by internal and external environmental conditions (McCallum, 1902; Ashby, 1948b; Allsopp, 1955; Jones, 1956). Thus, the shape of leaves on different parts of the stem of the same plant is apparently influenced by internal factors. Among the external factors that influence the shape of leaves are water supply, nutrients, day length, amount of light, etc.

DEVELOPMENT OF THE VEINS

The development of the vascular system in the leaf has, as yet, been studied only in a small number of plants. From what is known of the development of dicotyledonous leaves, it appears that development of the procambial strand of the mid-rib precedes that of the lamina and it proceeds in the acropetal direction (Fig. 106, no. 5). With the commencement of the development of the lamina the procambial strands of the large lateral veins and, later, of the smaller veins begin to form gradually. As was seen in *Nicotiana tabacum* (Avery, 1933), the procambial strands of the small veins, which form in a basipetal direction, develop mainly during the intercalary growth of the lamina (Fig. 105, nos. 4, 5). However, deviations from the above pattern of differentiation are also known to occur (Slade, 1957).

In the leaves of *Zea* (Sharman, 1942) the procambial strands of the median vein and of the principal lateral veins develop acropetally while those of the smaller lateral veins, which are arranged alternately with the larger ones, develop basipetally, i.e. from the tip to the base of the leaf. The latter development takes place only after the appearance of protophloem in the larger veins. The cross veins which connect the parallel veins are the last to form and they develop basipetally. The procambial strands of the marginal veins of the banana leaf also develop in a basipetal direction. The differentiation of the conducting elements begins before the completion of the procambial system. The protophloem and protoxylem both differentiate acropetally and the differentiation of the protoxylem follows that of the protophloem. After the final elongation of the veins, the development of the metaphloem and metaxylem commences in a more or less definite basipetal direction, first in the large strands in

which the differentiation of the protophloem and protoxylem is completed, and then in basipetally developing procambial strands, in which protophloem and protoxylem do not develop.

The blind vein-endings occurring in the areoli are, according to Slade (1957, 1959), caused by the rupture of the minor vascular network during that stage of development when the leaf expands as a result of mesophyll cell enlargement. According to Pray (1963), however, the vein-endings do not result from rupture, but there is a progressive differentiation of procambium from the ground meristem during the expansion of the lamina.

Development of leaves differing from the typical

Cataphyll formation in the shoot apices of the dicotyledons is indicated in the early stages of development of the primordium. Cataphylls are distinguished from foliage leaves by the following characteristics: the slightly developed mesophyll which is usually devoid of palisade parenchyma; the reduced system of vascular bundles which often form an open dichotomous type of venation; and the small number or even absence of stomata. In certain cataphylls there is very little, and sometimes even no sclerenchyma, while in others there is an excessive development of sclerenchyma. In some plants, such as *Aesculus*, for example, a periderm develops below the abaxial epidermis of the outer scales.

The following are the differences that take place in the development of the cataphyll as compared with that of a foliage leaf: the adaxial meristem of the leaf axis primordium is only slightly active or not at all; the marginal growth is accelerated and is truly lateral and not latero-adaxial, as in the foliage leaf; as a result of rapid growth and the absence of thickening of the mid-rib the scale becomes typically sheath-like.

MONOCOTYLEDONOUS LEAVES

Grass leaves have linear laminae and sheathing bases surrounding the stem. The development of the leaf of *Oryza sativa* as described by Kaufman (1959) will be used here as an example of the development of this type of leaf.

The leaf primordia are initiated in the tunica from which the ground meristem and protoderm of the leaf develop. At the shoot apex, in the early stage of initiation, a localized protuberance appears which later becomes crescent-shaped and then as a result of further marginal and apical growth, eventually surrounds the apex. As the young primordium grows upwards it becomes hood-shaped (Fig. 109, no. 1). Apical growth of the leaf ceases during the third plastochron when the primordium is

about 0·9 mm long, but the margins continue to grow and the primordium elongates further. The continued marginal growth is brought about by the activity of the marginal meristem and the elongation of the primordium by a rib-meristem form of growth. A meristem of this kind is characterized by parallel series of cells in which transverse divisions take place. The rib meristem and adaxial meristem (Fig. 104, no. 3) become distinguishable during the second and third plastochrons.

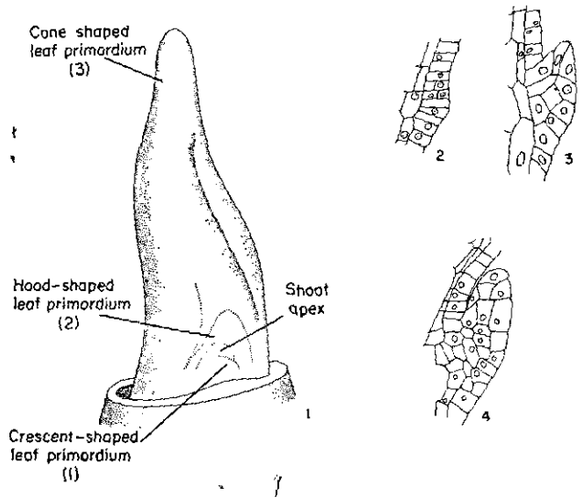

FIG. 109. 1, Three-dimensional drawing of the shoot apex of *Oryza*, showing the apex and first three leaf primordia. Numerals indicate the relative plastochrons. 2–4, Median longitudinal sections of ligules at different stages of development (Adapted from Kaufman, 1959.)

As described above, in the primordia of monocotyledonous leaves, the processes of apical and marginal growth are simultaneous during the early plastochrons. This is contrary to the development of dicotyledonous leaves where there are two distinct stages as have been previously described (Esau, 1953; Kaufman, 1959).

In *Oryza* the ligule is initiated during the third plastochron by periclinal divisions in the adaxial protoderm (Fig. 109, nos. 2–4). At first the ligule is a small adaxial protuberance which, as a result of continued periclinal divisions in the protoderm, expands laterally towards the margin of the sheath. The auricular primordia are apparently derived from both the sheath and ligule protoderm as well as from the ground meristem.

Continued elongation of the lamina and sheath, at this stage, still results from the activity of the rib meristem, whereas the extension of the lamina wings is caused by the activities of the marginal and of the distinct plate meristems.

The development of the sheath differs from that of the lamina in that no distinct plate meristem is seen in the wings of the sheath and the extension of them is accomplished, primarily, by the activity of the marginal meristem and by the enlargement of the cells derived from it.

As the differentiation in the lamina precedes that in the sheath, the meristematic activity becomes more and more restricted to the base of the sheath where the region of actively dividing and enlarging cells should, therefore, be regarded as an intercalary meristem.

The direction of the cellular differentiation and maturation in the leaf of *Oryza* and *Musa* is basipetal. The development of the laminar mesophyll in the former is depicted in Fig. 108, no. 2.

In certain monocotyledons the apical meristem of the primordium ceases its activity very early and then a new centre of growth arises on the abaxial side of the original leaf apex. That part of the leaf that develops from the new apex is *unifacial* as it consists of tissues from the abaxial side of the leaf only (Knoll, 1948; Thielke, 1948). The unifacial part of the leaf may be cylindrical, as for instance in *Allium cepa* and *Juncus maritimus*, or it may be flat, as in *Iris* (Fig. 92, no. 2).

Leaf abscission

In perennial and especially woody plants with distinct seasonal growth rhythms, there is a seasonal drying-out and loss of organs. This loss is brought about by the process of *abscission*. Leaves, floral parts, fruits and branches, for example, in *Ulmus* and *Populus* (Eames and MacDaniels, 1947), may thus be shed.

Leaves of gymnosperms and woody dicotyledons are usually shed prior to their death as a result of changes that take place in the tissues of the leaf base. In the base of mature deciduous leaves a narrow zone, the so-called *abscission zone*, can be seen. This zone can be distinguished, histologically from the surrounding tissues because of its different structure (Fig. 110, nos. 1, 2) and externally by the presence of a shallow groove or by a difference in colour of the epidermis. The vascular bundles in this region are usually narrower and the sclerenchyma and collenchyma are less well developed or absent. Some days or even weeks prior to the shedding of the leaf abscission tissue, termed the *separation layer*, develops in this zone. This tissue consists of a few layers of cells which are generally distinguishable from the neighbouring cells by their shape, smaller size, containing many starch grains, having a dense cytoplasm as well as by different wall staining properties. Generally, cell divisions can be observed in the region destined to form the abscission tissue. A short time before the leaf is shed the middle lamellae alone, or the middle lamellae together with the outer layers of the walls of these cells, become gelatinous and even-

tually they disintegrate and dissolve resulting in abscission. Sometimes even entire cells disintegrate. In some species no dissolution takes place and abscission is apparently effected by physical stresses. The latter is the case in most monocotyledons and herbaceous dicotyledons. In guayule (*Parthenium argentatum*), for example, the separation layer consists of suberized cells, but it is not directly involved in the separation of the leaf

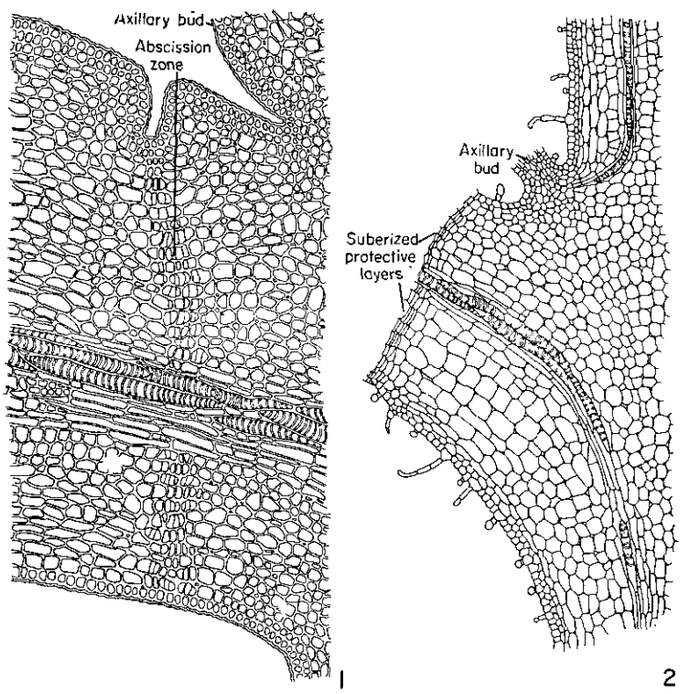

FIG. 110. Leaf abscission. 1, Longitudinal section of the leaf base of *Prunus* showing the cells that divide to form the separation layer. 2, *Coleus*, longitudinal section of portion of the stem together with the leaf base after the abscission of the leaf. (Adapted from Gibbs, 1950.)

from the stem. After the leaf dies its base breaks away from the stem through the weakened region of the abscission zone (Addicott, 1945; Facey, 1950; Addicott and Lynch, 1955).

All the parenchyma cells including those of the vascular tissues of the abscission zone take part in the process of abscission so that the leaf remains attached to the stem only by the vascular elements. According to many investigators these elements eventually break as a result of the weight of the leaf or the action of the wind and so the leaf is shed. According to

Facey (1950) the middle lamellae between the cells of the vascular tissues also disintegrate.

The tissues below the separation layer, which become exposed to the air with the shedding of the leaf, are protected from desiccation and the entry of agents of disease by the formation of the *protective layer*. This layer may be of two types—primary protective layer or secondary protective layer, i.e. periderm. The primary protective layer is formed as a result of the lignification and suberization of the parenchyma cells in this region or of the cells arising from them by irregular cell divisions (Pfeiffer, 1928). An opinion exists that the substance appearing in the cell walls of the protective tissue, and which has been defined as lignin, is really wound gum which gives reactions similar to lignin (Hewitt, 1938).

The time at which the primary protective layer and periderm appear differs in different plants. This fact has resulted in the development of a complicated classification of abscission types (Pfeiffer, 1928).

Many factors exist that apparently influence the abscission of leaves, and growth regulators are the most important among them (Addicott and Lynch, 1955). It is known, for example, that auxin inhibits abscission (Gawadi and Avery, 1950).

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CHAPTER 13

THE ROOT

THE root constitutes the lower portion of the plant axis and it usually develops below the soil surface, although there are roots that grow in the air as there are stems that develop below soil surface. However, basic differences in the development and arrangement of the primary tissues in these two organs are always distinguishable. The histogenesis of the epidermis of the root differs from that of the stem (see Chapter 3). In spermatophytes the primary xylem in the root is exarch and that in the stem is endarch. The xylem and phloem strands in the root do not form common bundles but are arranged alternately, while in the stem the vascular bundles are collateral, bicollateral or amphivasal. Roots bear no appendages that are comparable to the leaves of the stem; roots are devoid of stomata and their branches originate in the relatively mature tissue of the pericycle in contrast to the stem where the branches originate from the apical meristem. Roots also possess a root cap which has no parallel in stems.

Much variability exists in the shape and structure of roots. This variability, in many cases, is related to the function of the roots, i.e. whether they are storage roots, succulent roots, aerial roots, pneumatophores, climbing roots, prop roots, or whether they contain symbiotic fungi (mycorrhiza). Environmental conditions often influence the root system. Plants growing in dry soils usually have better developed root systems. Many plants growing in sandy soils develop shallow, horizontal, lateral roots which spread out, close below the soil surface, over a distance of tens of metres (e.g. *Tamarix* and *Retama*).

On the basis of origin two types of roots—primary roots and adventitious roots—are distinguished. Primary roots develop from the apex of the embryo that is destined, from its origin, to give rise to a root, and from the pericycle of relatively mature parts of roots, while adventitious roots develop from other tissues of mature roots or from other parts of the plant body, such as stems and leaves. Special importance has been given to those adventitious roots that develop from the callus of cuttings.

In most dicotyledons and gymnosperms the root system consists of a tap root from which side branches arise. The order of appearance of the lateral roots is from the root neck (that part where the root joins the stem) towards the root tip, but in some cases the primordia of some of the lateral roots remain dormant. The mature portions of the root, which usually

undergo secondary thickening, function only as a holdfast in the soil and to store reserve materials. The uptake of water and salts is carried out mainly by the extremities of the root system which are still in the process of primary growth.

The roots of mature monocotyledons are usually adventitious and develop from the stem (Fig. 116, no. 1). They may branch several times, as do the roots of dicotyledons, or they may be unbranched, and generally such roots do not develop secondary thickening. The most common type of root system among monocotyledons is the fibrous root system. In grasses the adventitious roots begin to develop from the hypocotyl when the latter is still in the embryonic state, i.e. they are seminal roots.

The radicle present in the seed consists of the root meristem and it gives rise to the first root on the germination of the seed. In the gymnosperms and dicotyledons this root develops into the tap root with its branches. In monocotyledons this root usually dries out early in the growth of the plant and the root system of the mature plant consists of numerous adventitious roots.

The apical meristems of lateral roots develop deep within the inner tissues in contrast to the buds of the shoot which develop from outer tissues. Therefore the branching of roots is *endogenous* and that of stems, *exogenous*.

Cortical roots are present in several monocotyledons (Pant, 1943; McLean and Ivimey-Cook, 1951). In *Tillandsia*, for example, these roots, which originate in the pericycle of the stem, grow directly downwards through the cortex and they emerge near the base of the stem. In *Asphodelus tenuifolius*, contrary to most other herbaceous monocotyledons with fibrous root systems, the root developing from the radicle of the embryo persists, and a large number of cortical roots arise from the base of the flattened, condensed stem. The cortex of this primary root is penetrated by the adventitious cortical roots which pass vertically downwards through it for some distance before they emerge into the soil.

Arrangement of the primary tissues in the root

At a certain distance from the apical initials (see Chapter 3) of the root the following zones can be distinguished: *root cap*, *epidermis*, *root cortex* and *vascular* or *central cylinder*.

THE ROOT CAP

The root cap is situated at the tip of roots (Fig. 29, no. 2), it protects the root promeristem and aids the penetration of the growing root into the soil. The root penetrates into the soil more easily because of the mucila-

ginous nature of the walls of the outermost cells of the root cap. The root cap consists of living parenchyma cells which often contain starch. These cells may have no special arrangement or they may be arranged in radiating rows which originate from the initials. In many plants the central cells of the root cap form a more distinct and constant structure which is termed the *columella* (see Chapter 3).

The root-cap develops continuously. The outermost cells die, become separated from one another and disintegrate, and they are replaced by new cells which are produced by the initials. Root caps are apparently found on roots of all plants except for the roots of some parasites and some mycorrhizal roots. External factors influence the structure of the root cap. Root caps develop in true water plants but they degenerate early.

THE EPIDERMIS

The epidermal cells of roots are thin walled and are usually devoid of cuticle, although sometimes the outermost cell walls, including those of the root hairs, undergo cutinization (Guttenberg, 1940; Scott *et al.*, 1963). On those parts of roots that are exposed to the air and on those parts in the soil on which the epidermis persists for a long time, the outermost cell walls become thick, and may sometimes contain lignin or dark-coloured substances which have not been fully identified. The epidermis of roots is usually uniseriate but exceptions do exist. On the aerial roots of plants belonging to the Orchidaceae and in the epiphytic, tropical genera of the Araceae the epidermis is multiseriate and it is specialized to form a *velamen* (Fig. 67, nos. 3, 4). The velamen is a sheath of compactly arranged dead cells, the walls of which are strengthened by band-like or reticulate thickenings and which contain many primary pit-fields. When the air is dry these cells are filled with air, but when rain falls they become filled with water. Special structures, termed *pneumatodes*, are present in the velamen. The function of these structures is to enable gas exchange during these periods when the root is saturated with moisture. The pneumatodes consist of groups of cells with very dense spiral wall thickenings. These groups extend, in a ray-like fashion, from the periphery of the epidermis to the endodermis. Oil droplets can be discerned in these cells. The endodermal cells that are continuous with the pneumatodes are filled with air (Gessner, 1956).

The most characteristic feature of the root epidermis is the production of root hairs which are organs well adapted to the efficient uptake of water and salts. The region of root hairs is usually restricted to one or a few centimetres from the root apex. Root hairs are absent close to the apical meristem and they usually die and dry out on the more mature portions of the root. Certain herbaceous plants, and especially water-plants, lack root

hairs. Plants that usually grow in soil and which produce root hairs fail to do so when they are grown in water. Calcium is one of the factors controlling the normal development of root hairs (Cormack *et al.*, 1963). In some plants the root hairs remain on the root for a long time. In *Gleditschia triacanthos*, for example, the root hairs remain viable for some months and their walls become thickened. Long-lived root hairs have been found in certain species of the Compositae and in some plants of other families (Cormack, 1949; Scott *et al.*, 1963) but it is doubtful whether these root hairs take part in the uptake of water from the soil. In many cases the presence of such long-lived root hairs is connected with a small amount of secondary thickening and absence of periderm.

In certain plants all the epidermal cells may give rise to root hairs while in others only certain cells, *trichoblasts*, may do so. Some workers have found that root hairs develop from a subepidermal layer in the Commelinaceae and related families, and also in *Citrus* (Hayward and Long, 1942). (For more details see Chapter 10).

THE ROOT CORTEX

In most of the dicotyledons and gymnosperms the cortex of the root consists mainly of parenchyma cells. In many monocotyledons in which the root cortex is not shed while the root remains viable, much sclerenchyma develops in addition to the parenchyma. The root cortex is usually wider than the stem cortex (Fig. 112, no. 1) and therefore it plays a larger role in storage. The innermost layer of the cortex constitutes the *endodermis* (Fig. 111, nos. 1–3; Fig. 112, no. 2). In certain plants such as *Smilax*, *Iris* (Fig. 112, no. 1), *Citrus* (Cossman, 1940) and *Phoenix*, for example, there is a special layer below the epidermis; this layer is termed the *exodermis*.

The arrangement of the cells of the cortex, as seen in cross-section of the root, may be in radial rows, at least in the inner layers, or the cells of two adjacent concentric layers may be arranged alternately. The radial arrangement is the result of the way in which the cells divide during the formation of the cortex (Guttenberg, 1940; Heimsch, 1960). Repeated periclinal divisions increase the number of cell layers in a radial direction, while anticlinal divisions add to the periphery and length of the cortex. The cells that undergo periclinal divisions are the inner cortical cells and, after the periclinal divisions are completed the innermost layer of the cortex differentiates to form the endodermis.

Schizogenous intercellular spaces, which appear in the early ontogenetic stages, are very common in the root cortex. In certain plants, such as the Gramineae and Cyperaceae, large lysigenous intercellular spaces often develop in addition to the schizogenous ones. Large air canals are common in the root cortex of the Palmae (Tomlinson, 1961).

The parenchyma cells of the root cortex usually lack chlorophyll. Chloroplasts are found in the roots only of certain water plants and in the aerial roots of many epiphytes. Secretory cells, resin ducts and laticifers are found in the root cortex of different plants. If sclerenchyma is developed it is usually in the form of a cylinder within the epidermis, within the exodermis or adjacent to the endodermis.

In many gymnosperms and certain dicotyledons, such as plants belonging to the Cruciferae, Caprifoliaceae and Rosaceae, reticulate or annular wall thickenings can be found in the cells outside of the endodermis. Collenchyma is sometimes also found in the root cortex (Guttenberg, 1940).

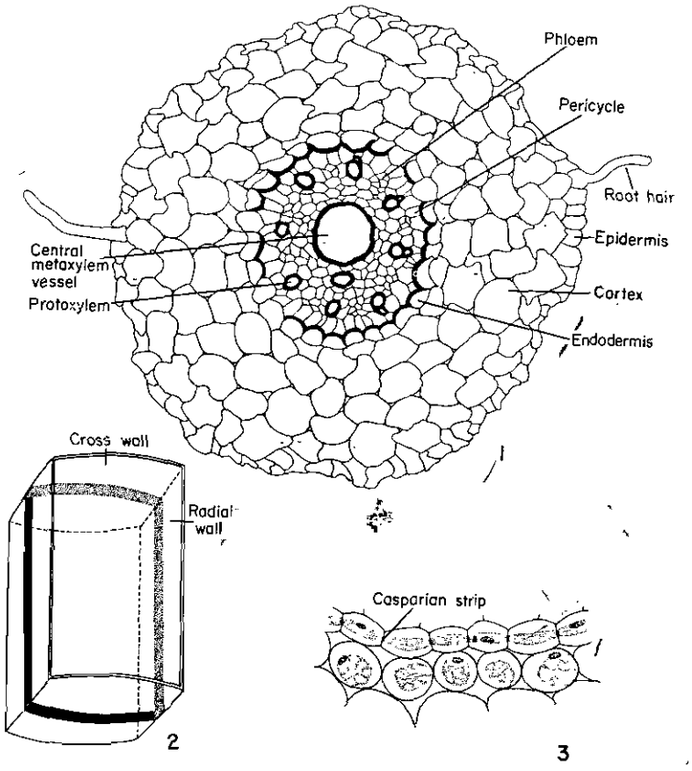

FIG. 111. 1, Cross-section of a root of a seedling of *Triticum*. 2, Three-dimensional diagram of a single endodermal cell with Casparian strip. 3, Portion of a cross-section of a root showing part of the endodermis and a row of cortical parenchyma cells in a state of plasmolysis. It can be seen that the protoplast of the endodermal cell remains attached to the Casparian strips. (No. 1, adapted from Avery, 1930; no. 3, adapted from Esau, 1953.)

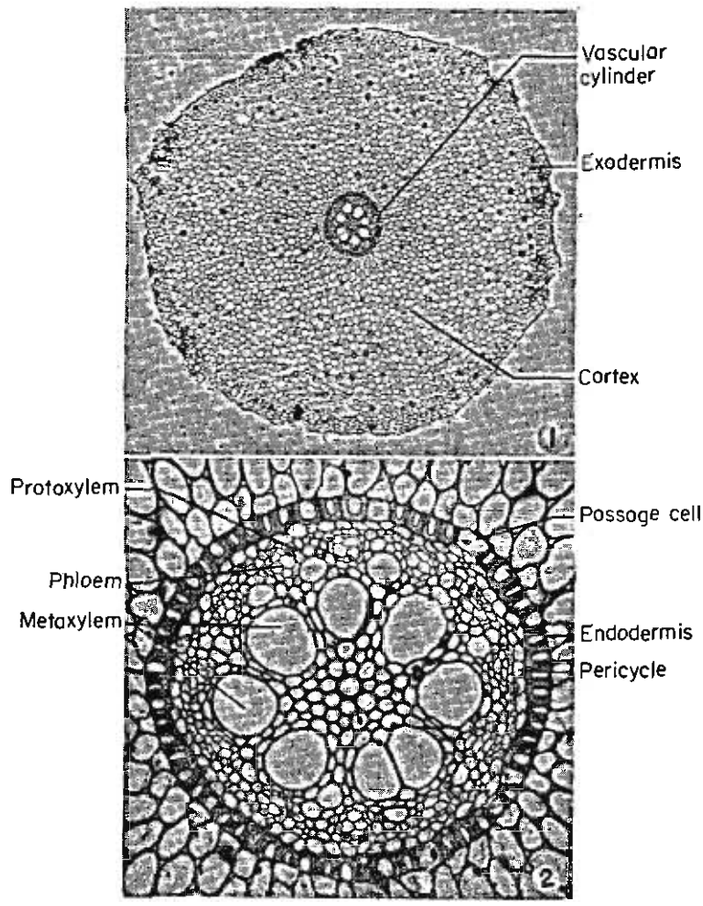

FIG. 112. Micrographs of cross-sections of the root of *Iris*. 1, Entire cross-section. ×10. 2, Vascular cylinder, enlarged. ×110.

THE EXODERMIS

In many plants the walls of the cells of the outer subepidermal layers of the cortex become suberized. In this way the exodermis, a protective tissue, is formed (Guttenberg, 1943). The exodermis is similar in structure and cytochemical characteristics to the endodermis (Van Fleet, 1950). An almost continuous suberin lamella lines the primary cell wall internally, and it in turn is usually lined with layers of cellulose which develop centripetally. Also lignin is often deposited in the walls of these cells and, in

certain cases, Casparian strips have also been distinguished (Van Fleet, 1950). The cells of the exodermis contain viable protoplasts even when mature. In the pteridophytes no exodermis is developed, but sometimes, as, for instance, in *Ophioglossum*, certain fatty substances are deposited in the walls of the subepidermal cells but no special suberin lamella is formed.

The thickness of the exodermis varies from a single cell layer to many layers. The exodermis may sometimes be accompanied, on its inner side, by sclerenchyma as, for example, in the root of *Ananas* (Krauss, 1949). In *Phoenix* the exodermis is fibrous (Tomlinson, 1961).

THE ENDODERMIS

The endodermis, which consists of a uniseriate cylinder of cells, develops in all vascular plants apart from a few exceptions. This layer of cells represents the inner boundary of the root cortex (Fig. 111, nos. 1–3; Fig. 112, no. 2). Because of its physiological and phylogenetic importance the endodermis has been very thoroughly investigated. In that part of the root where the primary vascular system is starting to mature, *Casparian strips* appear on the radial and cross walls of the endodermal cells (Fig. 111, no. 2). These strips are bands of wall substance that undergo chemical changes and which become thickened. If plasmolysis is brought about in endodermal cells in this stage of development the protoplast withdraws from the tangential walls, but remains attached to the Casparian strips (Guttenberg, 1943). The chemical composition and the structure of the Casparian strips has not yet been finally clarified but there is evidence that they contain both lignin and suberin (Van Fleet, 1942a). During the primary development of the root the endodermal cells are capable of much additional growth. This feature is striking during the endogenous initiation of lateral roots from the pericycle which is accompanied by the division and stretching of the neighbouring endodermal cells. In addition, the endodermal cells in certain roots continue to divide anticlinally during the early stages of secondary thickening. Casparian strips develop in many of the cells thus formed.

In many of the angiosperms, pteridophytes and some gymnosperms, the endodermis remains in the primary form and is shed together with the cortex with the development of secondary thickening and periderm. However, in other angiosperms in which there is no secondary thickening an almost continuous lamella of suberin develops on the inner side of the entire primary wall, including the Casparian strips. This lamella characterizes the second stage of development of the wall and in the third stage a layer of cellulose is laid down centripetally on the inside of the suberin lamella. This layer may reach a very considerable thickness on

the radial walls, the walls parallel to a cross-section of the root, and on the inner tangential walls of the endodermal cells (Fig. 112, no. 2). This type of endodermal cell is common in the roots of most monocotyledons (Guttenberg, 1943). These thickened endodermal cell walls may become lignified. The endodermis of the conifers is characterized by the second stage of wall development only, i.e. by the development of a suberin lamella on the inner side of the walls (Guttenberg, 1941; Wilcox, 1962a).

The additional wall layers of the endodermal cells do not develop simultaneously in all the endodermal cells as seen in a single cross-section. Casparian strips and the sucessive stages of the development of the typical wall first appear opposite the phloem strands from where the development spreads towards those endodermal cells that are opposite the xylem strands (Van Fleet, 1942a, b; Guttenberg, 1943; Clowes, 1951). Because of the delay in wall differentiation of the endodermal cells opposite xylem these cells often have Casparian strips only. These cells are termed *passage cells* as they are thought to provide passage for substances between the cortex and vascular cylinder. The passage cells may remain unaltered throughout the entire life of the root or they, too, may develop thick secondary walls as do the other endodermal cells.

The production of the suberin lamellae on the endodermal cell walls results from the polymerization of unsaturated fatty compounds which is brought about by oxidases and peroxidases. The peroxidases are brought to the endodermal cells via the sieve elements. This has led Van Fleet (1942b) to suggest that this is the reason why the greatest amount of suberin is laid down on the inner walls of the endodermal cells and why the passage cells, which lack suberin, appear mostly opposite the xylem, and not the phloem, strands.

THE VASCULAR CYLINDER

The vascular cylinder occupies the central portion of the root. In roots it is more clearly delimited from the cortex than in the stem, because of the presence of the endodermis which is characteristically better developed in roots.

The primary vascular tissue is surrounded by a region of cells which is termed the *pericycle* (Fig. 112, no. 2). The pericycle generally consists of one or more layers of thin-walled parenchyma cells. It is in direct contact with the protophloem and protoxylem and can already be distinguished prior to the lignification of the protoxylem elements. The pericycle retains its meristematic characteristics. The primordia of the lateral roots in all spermatophytes and the phellogen and portions of the vascular cambium in the dicotyledons develop from the pericycle. In monocotyledons the phellogen usually develops in the outer parts of the cortex. In the roots

of many Gramineae and Cyperaceae the outermost tracheary elements of the protoxylem may develop from the pericycle and, in the Potamogetonaceae, even the phloem elements may do so. In such cases the pericycle is not continuous (Guttenberg, 1943).

In monocotyledons, where there is usually no secondary thickening, sclerification takes place in part or all of the pericycle. In most angiosperms the pericycle is uniseriate but in many monocotyledons (such as the Gramineae, Palmae, *Agave* and *Smilax*) and in a few dicotyledons (such as *Celtis*, *Morus* and *Salix*) the pericycle consists of several layers of cells. Sometimes the pericycle is uniseriate opposite the phloem and is wider opposite the xylem. In gymnosperms the pericycle is usually multiseriate. In the roots of certain water-plants and parasites the pericycle is absent. Laticifers and secretory ducts may be present in the pericycle.

One of the principal features by which roots and stems can be differentiated is the arrangement of the primary vascular tissues. In the primary body of the root the pericycle is bordered directly on its inner surface by the phloem and xylem strands (Fig. 112, no. 2; Fig. 114, no. 1). The phloem strands are always separate and they are concentrated on the periphery of the vascular cylinder. The xylem strands may be in separate units on the periphery of the vascular cylinder or they may extend into the centre and then, as in many plants, the xylem appears star-shaped in cross-section. This structure led many workers to regard the vascular cylinder of the root as being a protostele. In many plants, and especially in the monocotyledons, the xylem strands do not reach the centre of the vascular cylinder which is then occupied by a pith.

The tracheary elements in the root mature centripetally and therefore the xylem is exarch, i.e. the protoxylem is situated on the outer side of the metaxylem. The differentiation of the phloem is also centripetal so that the protophloem is closest to the pericycle, while the metaphloem is closest to the axis of the root.

The number of protoxylem groups in the root, i.e. whether one, two, three, etc., is expressed by the terms *monarch*, *diarch*, *triarch*, respectively, and a root in which there are many protoxylem groups is said to be *polyarch*. Diarch roots (Fig. 115, no. 1) are found, for example, in *Lycopericon*, *Nicotiana*, *Beta*, *Raphanus*, *Daucus* and *Linum*. In *Pisum* the root is triarch, while in *Vicia* (Fig. 113, no. 2), *Ranunculus* and *Gossypium*, it is tetrarch. Polyarch arrangement is characteristic of the adventitious roots of monocotyledons (Fig. 112, no. 2). A correlation exists between the diameter of the vascular cylinder and the number of protoxylem groups and the presence or absence of a pith. When the diameter of the vascular cylinder is large a pith is usually present and the number of protoxylem groups is large. Variations in these features may be found even in one and the same plant. For example in one plant of *Libocedrus decurrens* di-, tri-, tetra-, penta- and hexarch roots have been found (Wilcox, 1962b).

Similar variation has been observed in certain dicotyledonous species (Jost, 1932; Torrey, 1957).

In gymnosperms and dicotyledons the number of the xylem strands in the root is generally small. In these groups of plants the roots are usually di-, tri- or tetrarch but there are some dicotyledonous species in which there are more xylem strands. The water-plant, *Trapa natans*, has a thin root which is *monarch*. In monocotyledons the number of xylem strands in the seminal roots is small, like that in dicotyledonous roots, but the

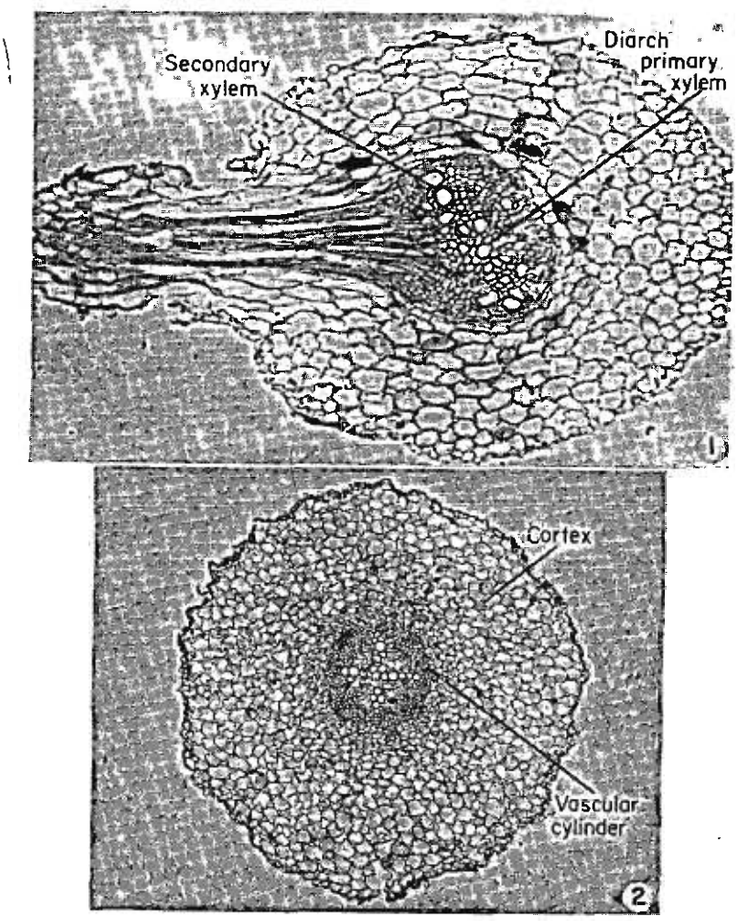

FIG. 113. Micrographs of cross-sections of roots. 1, *Lycopersicon esculentum* in which the development of a lateral root can be seen. ×70. 2, A young root of *Vicia faba*. ×40.

adventitious roots are polyarch and the number of strands in the Palmae and the Pandanaceae may be 100 or more. In the roots of the Filicinae different numbers of xylem strands may be found—from one, as in *Ophioglossum lusitanicum*, to many as in *Marattia fraxinea*.

In certain monocotyledons, such as *Triticum* (Fig. 111, no. 1), one large vessel is found in the centre of the vascular cylinder. Between this meta-

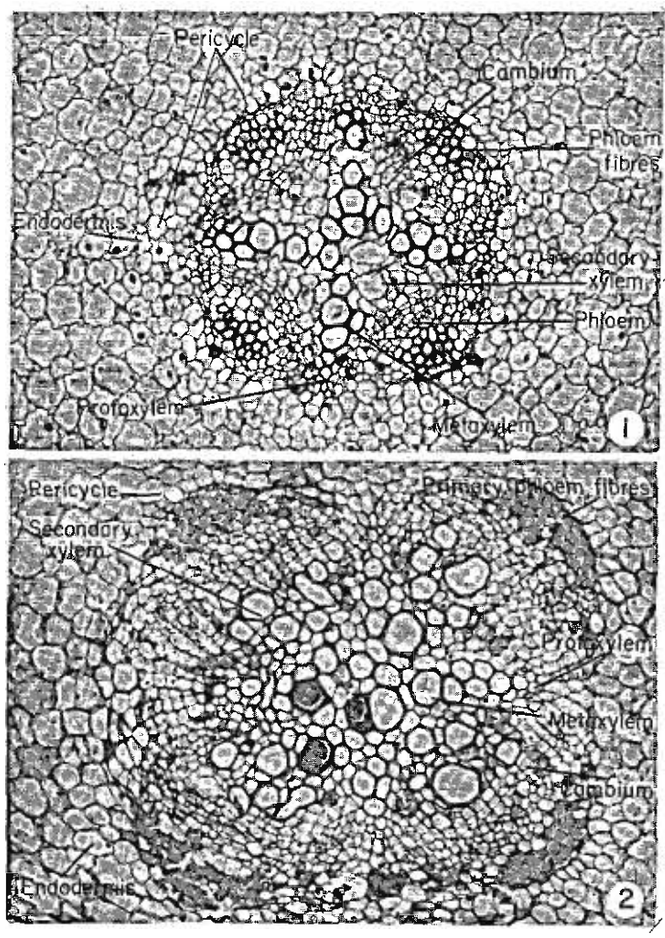

FIG. 114. 1, Micrograph of a cross-section of the tetrarch vascular cylinder of a young root of *Vicia faba* in which recently formed elements of secondary xylem, still thin-walled, can also be distinguished. ×115. 2, As above, but of an older root in which a relatively large amount of secondary xylem has been formed and in which the cambium is already almost cylindrical. ×115.

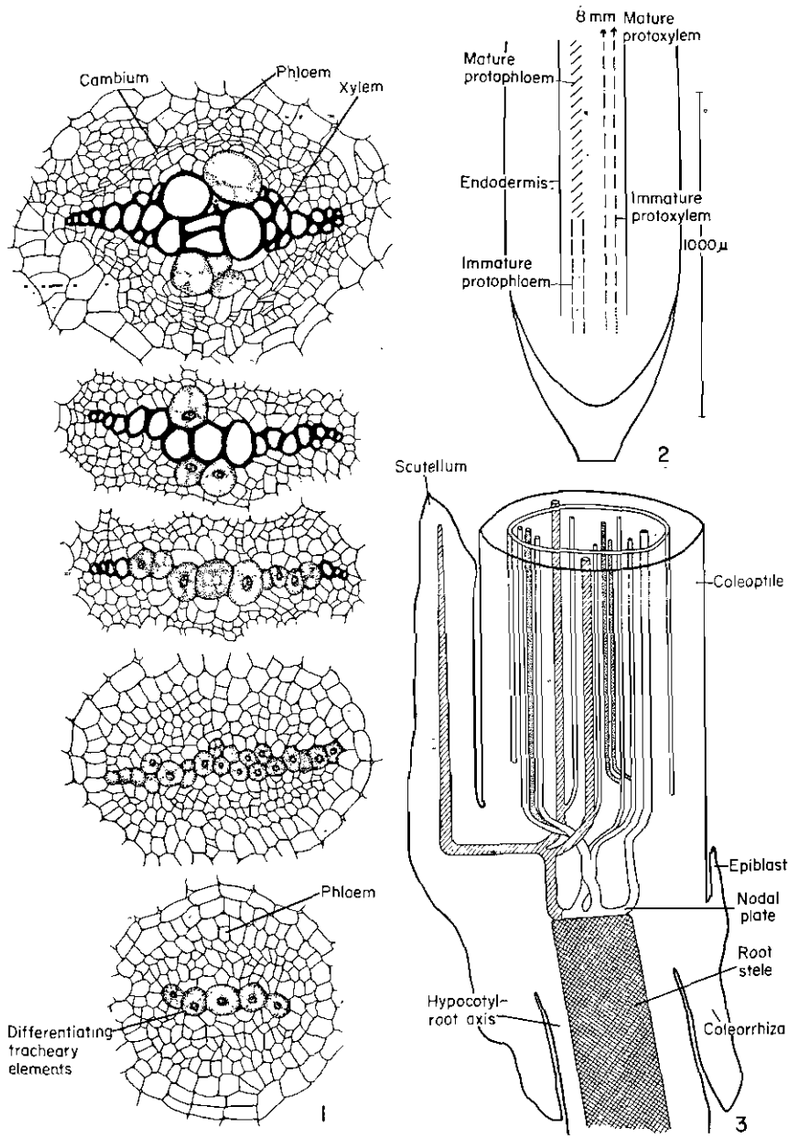

FIG. 115. 1, Cross-sections, at different levels, of a root of *Raphanus sativus* showing the differentiation of the primary xylem. 2, Diagram of a longitudinal section of the root tip of *Hordeum* showing the areas of differentiation and maturation of the vascular tissues. 3, Three-dimensional diagram of a portion of a seedling of *Triticum* showing the connection of the vascular systems of scutellum, hypocotyl-root axis, coleoptile and the first foliage leaves. (No. 1, adapted from Stover, 1951; no. 2, adapted from Heimsch, 1951; no. 3, adapted from Boyd and Avery, 1936.)

xylem vessel and the peripheral strands there is usually parenchyma. In other plants, e.g. *Zea* and *Iris* (Fig. 112, nos. 1, 2) the large metaxylem vessels form a circle around the pith. The number of these large vessels is not always equal to that of the peripheral strands. In certain plants two peripheral xylem strands are associated with a single large inner vessel. In woody monocotyledons the inner vessels may be arranged in two or three circles (e.g. *Latania* of the Palmae) or they may be scattered in the centre of the cylinder (e.g. *Raphia hookeri*). In a few other monocotyledons, e.g. *Musa*, *Cordyline* and *Pandanus*, phloem strands are scattered in the centre of the root.

In most plants there are interconnections between the different tracheary elements which appear separate in cross-section of the root. In roots with a pith it is also possible to find, here and there, lateral connections between the phloem groups. However, there are plants that have no lateral connections between the phloem strands or the different tracheary elements.

The primary phloem of the roots of most plants does not contain fibres but in certain plants, such as those of the Papilionaceae, Malvaceae and Annonaceae (Guttenberg, 1943), fibres are found in the primary phloem (Fig. 114, nos. 1, 2).

In many mature roots that do not have secondary thickening the parenchyma, associated with the primary vascular tissues, becomes sclerified. In many Coniferales, except for the Taxodiaceae, Cupressaceae and Taxaceae, resin ducts are present in the region of the primary conducting tissues.

Some roots are polystelic. In cross-sections of such roots a number of vascular cylinders each of which is surrounded by an endodermis can be seen. Examples of such roots are the root tubers of some species of *Orchis* (Arber, 1925) and members of the Palmae (Tomlinson, 1961).

Tissue differentiation in the root

Some distance from the apical promeristem of the root the epidermis, cortex, and vascular cylinder can be distinguished. The pericycle can also be identified close to the apical meristem. As it is not possible to distinguish clearly between the meristems of the vascular and non-vascular tissues in the vascular cylinder, it is not yet clear whether the pericycle develops from the procambium or from the ground meristem. The cells of the procambium that differentiate into the tracheary elements soon become distinguishable from those cells from which the phloem elements will develop. The former cells enlarge and they have large vacuoles, while the latter undergo numerous divisions without enlarging so that they become very small.

The order of appearance of the different tracheary elements, in comparison to the order in which they undergo maturation, is of interest. The

cells that develop into metaxylem elements enlarge, together with the vacuoles in them, prior to those cells that differentiate into the protoxylem elements while the order of maturation is, of course, the contrary. Therefore the final dimensions of the metaxylem elements are far larger than are those of the protoxylem. This is especially obvious in the monocotyledons (Heimsch, 1951).

The ontogenetic development of the primary vascular system of the root is simpler than that of the stem because the differentiation of the vascular system of the latter is connected with the development of the leaves. The vascular system of the root develops independently of the lateral organs and the procambium develops acropetally as an uninterrupted continuation of the vascular tissues in the more mature parts of the root. The differentiation and maturation of the xylem and phloem is also acropetal (Popham, 1955) and follows that of the procambium. From the accurate investigations that have been carried out till now it appears that the protophloem elements mature closer to the apical meristem than do the earliest tracheary elements (Fig. 115, no. 2). From this it is seen that the process of maturation of the protoxylem and protophloem elements is also simpler in the root than in the stem where the early differentiation of the xylem close to a leaf primordium is in two directions.

Generally the differentiation of the root tissues behind the apical promeristem can be summarized as follows: periclinal divisions in the cortex cease near the level where the sieve elements mature; beyond this region the root undergoes rapid elongation, and the maturation of the protoxylem usually takes place only when the process of elongation is almost completed; Casparian strips develop in the endodermal cells before the maturation of the protoxylem elements and generally also before the appearance of root hairs.

The proximity of the mature conducting elements to the root apex is dependent on the rate of growth and both these processes are dependent on the external conditions, the type of root, and the stage of its development (Wilcox, 1962a). Heimsch (1951) found the following distances between the root apex and the first mature vascular elements in different roots of *Hordeum:* protophloem elements, 0·25–0·75 mm; protoxylem elements, 0·40–8·5 mm; elements of the early metaxylem, 0·55–21·6 mm or more, while the large central vessels mature at even greater distances (Fig. 115, no. 2). The earliest appearance of Casparian strips is at a distance of about 0·75 mm from the apex.

CAMBIUM IN ROOTS

There is great variation in the secondary growth in different roots. The tap-root and main lateral roots of gymnosperms and woody dicotyledons usually have secondary thickening, but the smallest branches do not. In

the roots of some herbaceous dicotyledons secondary thickening may be completely absent, vestigial (e.g. *Ranunculus)* or it may be well developed (e.g. *Medicago)*.

Roots of most monocotyledons are devoid of secondary thickening. However, in some, e.g. *Dracaena*, such thickening does occur.

In the roots of gymnosperms and dicotyledons that do exhibit secondary thickening the cambium first appears on the inner side of the phloem (Fig. 114, no. 1). After these cambial cells have produced a few secondary elements the pericycle cells on the outer sides of the protoxylem groups begin to divide, and the inner cells resulting from these divisions form cambial cells. These strands of cambium unite with those on the inner sides of the primary phloem strands. At first the cambium has an undulating shape, as seen in cross-section of the root; but as the development of the secondary xylem on the inner side of the phloem strands precedes that of the secondary xylem external to the protoxylem groups, the cambium soon becomes circular in cross-section (Fig. 114, no. 2).

DEVELOPMENT OF LATERAL ROOTS

As has already been mentioned, one of the most prominent characteristics by which roots and stems can be distinguished is the manner in which the lateral appendages develop from the axis. In the stem, the primordia of the branches and leaves are initiated in the apical meristem from the outer cell layers. Unlike this, lateral roots develop endogenously from inner cell layers in regions of relatively mature tissues. The initiation of lateral roots usually commences immediately behind the region of root hairs; but in certain plants, especially water-plants, e.g. *Eichhornia*, the lateral roots begin to form, in the young pericycle, below this region. In gymnosperms and angiosperms the lateral roots are commonly initiated in the pericycle whence they pass through the cortex of the parent root to the exterior. In pteridophytes the lateral roots mostly are initiated in the endodermis (Ogura, 1938).

A definite relationship exists between the position of the protoxylem groups and phloem strands and the position of the initiation of lateral roots. In triarch roots or those with more than three protoxylem groups the lateral roots usually develop opposite the protoxylem groups. But in certain plants, for instance, species of the Gramineae, Cyperaceae and Juncaceae, the lateral roots develop opposite the phloem strands. In diarch roots the primordia of the lateral roots appear opposite the phloem strands or close to the protoxylem groups (Fig. 113, no. 1), and so two rows of lateral roots develop. In some diarch roots, lateral roots may develop on both sides of the protoxylem groups so that, in such cases, four rows of lateral roots develop. In the fleshy carrot root additional lateral roots develop at

the base of earlier-formed lateral roots that have dried out (Esau, 1940, 1953).

In angiosperms the primordia of the lateral roots are formed by the periclinal and anticlinal divisions of a group of pericycle cells. The initiating divisions are periclinal. As a result of further growth the primordium penetrates through the cortex of the parent root. It is possible to distinguish the zones of primary tissues, apical meristem and root-cap of the lateral

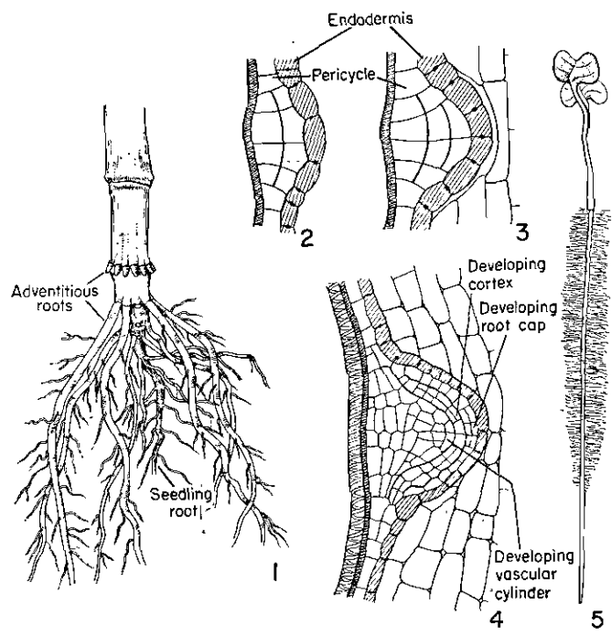

FIG. 116. 1, Basal portion of a plant of *Zea mays* in which the remains of the seedling roots, and the adventitious roots, arising at the base of the internodes, can be seen. 2–4, Portions of radial longitudinal sections of roots of *Hypericum* showing early stages in the development of lateral roots. 5, A seedling of *Sinapis alba* in which the region of root hairs can be seen. (Adapted from Troll, 1948.)

root primordium even before it appears on the surface of the parent root (Fig. 116, nos. 2–4). Different opinions exist as to how the passage of the growing lateral root is effected through the cortex of the original root. According to one view the lateral roots partially digest the cortical tissue during penetration, while according to another view the process of penetration is purely a mechanical one. However, it is generally agreed that the developing lateral roots do not form any connection with the tissues through which they penetrate.

In many plants, as, for instance, *Daucus carota*, the endodermis of the parent root takes part in the formation of the primordium of the lateral roots (Esau, 1940). In such cases the endodermis may divide only anticlinally, but sometimes it may divide periclinally as well and thus forms more than one layer. With the eruption of the lateral root on the surface of the parent root, or even prior to it, the tissue that developed from the endodermis dies and it is eventually shed. In certain water-plants and in species of the Papilionaceae, Cucurbitaceae and some others families, the innermost layers of the cortex also take part in the development of the lateral roots (Esau, 1953).

The connection between the vascular systems of the lateral and parent roots is brought about by intervening cells. As the lateral roots originate in the pericycle the distance between the two vascular systems is small. Of the intervening cells, which also develop from the pericycle, some differentiate into sieve elements and some into tracheary elements.

The xylem of the lateral roots of many monocotyledons is connected with two or more xylem strands of the original root. This can be seen in *Monstera*, for example, where the connections are not only with the peripheral xylem strands but also with the innermost large vessels of the metaxylem. This is brought about by the modification, into tracheary elements, of parenchyma cells between the xylem and phloem strands (Rywosch, 1909).

Adventitious roots

Adventitious roots, as defined above, may develop from large roots, from the hypocotyl of young plants, from the primary and secondary body of stems, and from leaves. In the roots and stems of most plants adventitious roots develop endogenously, but there are examples in which the development is exogenous. Primordia of adventitious roots may be formed by the following tissues: the epidermis, together with cortical tissue, of buds and hypocotyls (e.g. *Cardamine pratensis*, *Rorippa austriaca*); stem pericycle (e.g. *Coleus*, *Zea mays*); ray parenchyma between pericycle and cambium (e.g. *Tropaeolum majus*, *Lonicera japonica*, *Tamarix*); non-differentiated secondary phloem and cambium between the vascular bundles (e.g. *Rosa*); interfascicular cambium and pericycle (e.g. *Portulaca oleracea*); interfascicular cambium, pericycle and phloem (e.g. *Begonia*); the pith of the stem (e.g. *Portulaca oleracea*); parenchymatous interruptions in the secondary xylem which are formed due to the presence of leaf-gaps (e.g. *Ribes nigrum*) or buds (e.g. *Cotoneaster dammeri*) (Hayward, 1938; Boureau, 1954); tissues of leaf margins and petioles (e.g. *Begonia*, *Kalanchoë*.)

The development of adventitious roots has been described in some species of *Salix* (Carlson, 1938, 1950). In these species the adventitious roots

develop from primordia which appear in the stem prior to its removal as a cutting. These primordia are formed from secondary parenchymatous tissue in the leaf- or branch-gaps. Several layers of cells external to the cambium take part in the formation of a primordium, to whose inner side cells are also added by the cambium. The primordium becomes dome-shaped as a result of the intensified growth of the secondary xylem immediately inwards of it. These primordia remain dormant within the inner bark as long as the branch is not removed from the tree. The differentiation of these primordia is extremely slow so that even in 9-year-old branches, the typical root-tip structure is not discernible. After the first year of growth, additional primordia may develop vertically above and below the first-formed primordia on both branches left on the tree and on cuttings. On cuttings most of the primordia develop rapidly into roots. Similar adventitious root primordia have been observed on woody roots of *Zygophyllum dumosum*.

Plant species differ from one another in their ability to produce roots on cuttings. Cuttings of plants with dormant adventitious root primordia (e.g. *Salix*) root easily as do many plants with broad vascular rays but without such primordia (e.g. *Vitis vinifera*, *Tamarix* spp.). Cuttings of *Ceratonia*, *Pyrus* and *Carya*, for example, which have no dormant primordia and in which the rays are narrow, root with difficulty.

The ability to produce adventitious roots varies with age—generally, they develop more easily on younger plants and plant organs.

Root structure in relation to function

RELATION BETWEEN STRUCTURE AND UPTAKE OF WATER AND SOLUTES

The uptake of water and solutes is accomplished mainly by the young parts of the roots.

The accepted opinion is that only a small amount of water penetrates through the root-cap and through the apical meristem (Kramer, 1945; Brouwer, 1959). The main uptake of water is apparently in that region where the primary xylem is almost completely mature. In this region the root hairs, the important role of which in the uptake of water is not doubted, are produced. In mature regions in which a periderm is present water uptake also takes place, and is probably effected through the lenticels (Kramer, 1946). The amount of water uptake in different places along the root depends on various factors. To a certain extent these differences are dependent on differences in structure. In many trees the region of uptake may become inactive with the onset of unfavourable ecological conditions as a result of the production of impermeable layers. The endodermis and sometimes the exodermis, both of which contain suberin

lamellae, develop a short distance from the apical meristem. In certain plants fatty substances have been found in the walls of the cells of the outer layers of the root-cap, and in the epidermal cells between the root-cap and that region where the exodermis begins to form. This process has been termed *metacutization* (Plaut, 1920; Guttenberg, 1943).

Ions are selectively transported and accumulated by roots. In the various processes involved the different tissues of the root participate in different ways. The undifferentiated non-vacuolated cells of the root apex (up to 0·5 mm in the root of *Zea mays*, for example) do not accumulate ions, and ions enter and leave the cells passively (Handley and Overstreet, 1963). The vacuolated and differentiated cells of the cortex have a marked ability to accumulate solutes. However, in different plants the main sites of entry of the various ions along the roots differ (Scott and Martin, 1962). The vascular cylinder, however, which serves as the main transport system for water and ions, exhibits a low rate of metabolism and has almost no capacity for accumulation.

The main barrier to transport across the root is believed to be the endodermis. It is assumed that the fatty substances, deposited in the Casparian strips of the endodermal cells, prevent the free passage of water and solutes through the cell walls and restrict all transport to the protoplast. It is well known that the cytoplasm of the endodermal cells is strongly attached to the Casparian strips. Therefore the passage of solutes from the cortex into the xylem through the free space is prevented (Priestley, 1920, 1922; Priestley and North, 1922; Brouwer, 1959). The endodermis not only takes part in selective transport of solutes from the outer solutions into the vessels, but also constitutes a barrier to water movement, thus making possible the existence of a hydrostatic pressure – usually termed the root pressure. The endodermal barrier appears to be very effective in ion selectivity except in cases where the ionic strength of the outer solution is very high or when the roots are deprived of energy sources.

STRUCTURE OF STORAGE ROOTS

In all primary roots reserve substances (mostly starch) are stored in the cortex, which in most plants is relatively thick. In ordinary roots with secondary thickening reserve substances are stored similarly as in stems, i.e. in the parenchyma and sclerenchyma tissues of the secondary xylem and phloem. Usually roots contain more parenchyma than do stems.

There are plants in which certain parts of the root system develop into thick, fleshy organs which function especially as storage organs. In many plants the tap-root and hypocotyl undergo such modification.

The origin of the storage tissue may differ. In the carrot, for example (Esau, 1940), the hypocotyl and tap-root become thickened and, with the

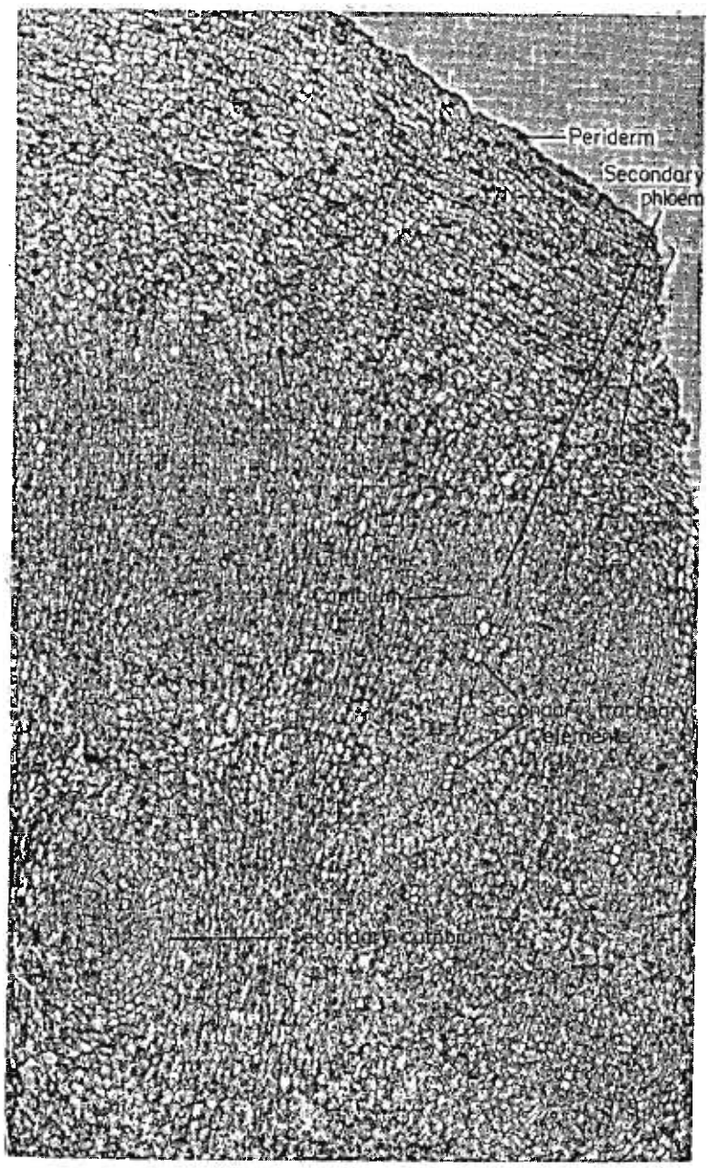

FIG. 117. Micrograph of the outer portion of a cross-section of the root tuber of *Ipomoea batatas*. ×20.

development of the periderm, the narrow cortex is shed. The organ becomes fleshy as a result of the excessive development of parenchyma in the secondary xylem and especially in the secondary phloem.

In the sugar beet, according to Artschwager (1926), the hypocotyl and root become fleshy as a result of an anomalous secondary thickening which is characteristic of the Chenopodiaceae and which is discussed in more detail in a later chapter. Here it will only be mentioned that, as a result of the activity of numerous cambia, layers of secondary tissue consisting of parenchyma in which groups of conducting elements are scattered, are formed. The sugar is found as a reserve substance in the cells of this secondary parenchyma.

In *Ipomoea batatas* (Fig. 117) the fleshiness of the root is due to the following development (Hayward, 1938). Both the primary and secondary xylem develop normally and contain a large amount of parenchyma. However, with further development many anomalous secondary cambia are formed around single vessels or groups of them. These cambia, which are annular in cross-section of the root, produce some phloem but mainly parenchyma. Some distance from the vessels, laticifers are also formed. Tertiary tracheary elements develop close to and around the vessels that are encircled by these special secondary cambia. Still later, secondary cambia may be formed in the parenchyma not associated with vascular elements.

In the radish the fleshiness of the root and hypocotyl is due to the excessive development of parenchyma in the secondary xylem which is produced by the normal cambium, as well as secondary parenchyma produced by additional cambia which also produce tertiary conducting elements (Hayward, 1938).

ROOTS AS ANCHORAGE ORGANS

The anchorage function of the root in the soil is aided by the following structural features: the branching of many lateral roots from a tap-root and the development of many adventitious roots in fibrous root systems; the growth of root hairs which are of great importance in young roots; the development of sclerified tissues (principally xylem) in the centre of young roots and the development of sclerenchyma in old roots.

CONTRACTILE ROOTS

The renewal buds of certain plants occupy a definite position within the soil or on its surface. This position is mostly obtained by the pull of special roots, which have been termed *contractile roots* (Rimbach, 1895, 1899, 1929, 1932; Arber, 1925; Bottum, 1941; Davey, 1946; Dittmer, 1948;

Galil, 1958, 1961). Such roots are known to exist on many herbaceous dicotyledons (e.g. *Taraxacum; Medicago sativa; Daucus, Trifolium, Oxalis,* sugar beet) and in many bulbous and cormous monocotyledons (e.g. *Phaedranassa chloracra, Hypoxis setosa, Bellevalia flexuosa, Gladiolus segetum, Colchicum steveni, Ixiolirion montanum, Muscari parviflorum, Allium neapolitanum).* Contractile roots or parts of roots are distinguishable from normal roots by their outer, wrinkled appearance.

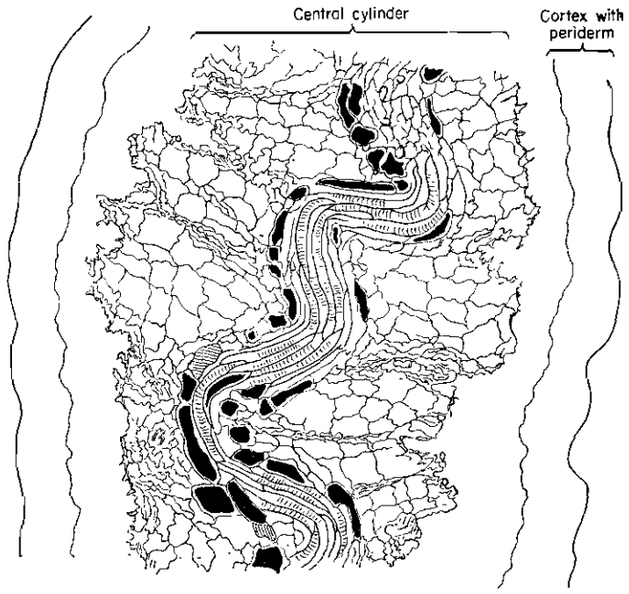

FIG. 118. Portion of a longitudinal section of a contractile root of *Oxalis hirta* showing the arrangement of turgid and collapsed cells in the contracted central cylinder, and the contorted xylem. Solid black cells represent secretory cells. (Adapted from Davey, 1946.)

According to Arber (1925), who studied *Hypoxis setosa,* only the outer cortex is wrinkled whereas the central cylinder and the inner cortex are unaffected. Rimbach (1899) and later investigators explain the shortening of the inner core as being due to the change in form of the inner cortical cells. These cells, according to them, increase in radial and tangential diameter and decrease in length.

Davey (1946) described the histological changes that are involved in the root contraction of *Oxalis hirta* seedlings. According to him a small amount of the contraction is due to the active growth of the phloem parenchyma cells in a transverse direction and their shortening in a longitudinal direction. The main contraction mechanism, however, is as follows: hori-

zontal zones of cells of the uniform secondary phloem parenchyma lose their protoplasts and sap and so collapse. Alternating with these zones of collapsing cells there remain narrow zones of living turgid cells. The vertical walls of the collapsing cells fold so that the horizontal walls are brought together. Each collapsing zone becomes inclined upwards so that the diameter of the root core becomes reduced and it tears away from the periderm and the remnants of the cortex. The cortical tissues then exhibit wrinkling. The phloem strands become contorted but remain alive. The xylem strands and their associated cambium become spirally contorted (Fig. 118).

Attention should be drawn, however, to the fact that the two above-mentioned mechanisms may not be the only ones acting in the root to bring about contraction.

ROOTS AS ORGANS OF AERATION

The root systems of trees growing in littoral swamps, in which the soil is periodically inundated and lacking in oxygen, exhibit various adaptations to their habitat. These involve features that ensure sufficient aeration and additional support.

The Rhizophoraceae are characterized by stilt-roots which descend from the stems and whose lower portions only are subterranean. The cortex of these stilt-roots is spongy due to the development of complex intercellular spaces (Metcalfe and Chalk, 1950). In *Phoenix paludosa* there are, at the base of the stem, special roots which descend into the mud and which contain lenticels and aerenchyma produced by the phellogen.

Aerial, negatively geotropic root projections, which are termed *pneumatophores*, are commonly produced in swampy habitats. These roots serve for gas exchange. In *Avicennia* the pneumatophores are erect, peg-like aerial projections of the lateral subterranean roots. In *Bruguiera eriopetala* knee-like aerial projections, which are part of the horizontal roots, are produced. The morphology and anatomy of the pneumatophores of *Amoora*, *Carapa* and *Heritiera* were studied in detail by Groom and Wilson (1925). In these genera the aerial projections are wing-like protuberances which are produced on the upper surface of the horizontal roots by intensified cambial activity in these regions. In the three last-mentioned genera it was seen that the pneumatophores all possess lenticels and that they contain only few xylem vessels and thick-walled fibres. The bulk of the tissue of the root consists of thin-walled fibres and parenchyma tissue (axial and ray parenchyma). At certain times this parenchyma was seen to contain much starch, and so it may sometimes act as a storage tissue. However, most of the cells have no solid contents and therefore it is possible that all the cells, including the vessels, may act as air reservoirs. In *Amoora* and *Carapa* the intercellular spaces in the wood are no larger than usual.

Adaptations of roots to xeric conditions

The following adaptations of roots to xeric conditions are well known: the form of the root system, the succulence of the roots, the development of a thick bark, the sclerification of the cortical cells, and the isolation of the vascular cylinder by periderm formation or by the necrosis of the cortical parenchyma (Hayden, 1919; Weaver, 1920; Evenari, 1938; Zohary and Orshan, 1954; Killian and Lemée, 1956). Secondary wall thickening in endodermal cells of ferns and monocotyledons was observed by Van Fleet (1957) to be more prominent in plants growing in unfavourable conditions. In addition to the above, there are other characters that may be of adaptive value.

One of the commonly accepted characters of xerophytes is the presence of well developed xylem tissues which help rapid conduction when water is available. In this connection it is of interest to mention the roots of *Retama raetam*. In this plant, which grows in sandy soils and wadi beds, there are in addition to the usual vertical and diageotropic roots, horizontal roots which have been observed to reach a length of up to 10 m. The vessel members of the vertical roots are narrower and shorter than those of the diageotropic roots and even more so than those of the horizontal roots. Moreover, in the latter type of root a gradient in the length and width of vessel members exists from the distal ends of the roots to the part where they are attached to the vertical roots. The advantage of this feature may be in its compensating effect on what would otherwise be a much more pronounced gradient in suction pressure from the stem toward the distal parts of the roots. Both the greater width and length of the vessel members in the distal parts of the horizontal roots presumably ensure a more efficient flow of water in these very long, horizontal roots. This feature is doubtless of great importance as the horizontal roots take up water from the upper layers, which in sandy soils, drain rapidly.

Two other interesting features have recently been observed in the primary roots of desert plants (Ginzburg, Ph.D. thesis). Firstly, in the roots of plants growing under extreme desert conditions the number of cortical layers is reduced. The advantage of this feature may be that it shortens the distance between the soil and the stele. Secondly, it has been observed that the Casparian strips are much wider in plants growing in extremely dry habitats and in salt marshes as compared with those growing under mesophytic conditions. In extreme cases the Casparian strips were seen to occupy the entire radial and tranverse walls of the endodermal cells. As has already been mentioned, it appears that the endodermis represents a semi-permeable barrier that controls the movement of solutes into the central cylinder. If this is correct, the endodermis would function more efficiently when the protoplasts are attached to larger portions of the radial and transverse walls of the endodermal cells. Such a feature seems, therefore, to be an adaptive character in plants growing under saline conditions.

Connection between the vascular systems of the root and stem

The primary vascular systems of the root and stem are distinguished from one another, as has already been described, by structure and by the direction of the radial development. The protoxylem in the root is exarch while that of the stem is endarch. The xylem and phloem are arranged alternately in the root, while the arrangement in the stem is usually collateral. Because of the differences in the functional design of the purely axial structure of the root and that of the appendage-bearing stem, there are necessarily basic differences in the pattern of the vascular systems of these two organs. The pattern of the vascularization of the stem, unlike that of the root, is determined by the presence of the leaves. At the level where the vascular systems of the root and stem meet, they must necessarily become adapted to one another. This region of the plant axis where one system gradually passes into the other has been termed the *transition region*. As has already been explained in an earlier chapter, in the embryo the shoot apex is found on one side of the hypocotyl and the root apex on the other. Therefore it is in the hypocotyl, and sometimes also in the lowermost internodes, that the one type of vascular system must change into the other.

The structure of the transition region is complex and differs in different plant species. Only general explanations are usually given of the transition between the conducting systems of the root and stem, and not of the transition between the conducting system of the root and the conducting system serving the cotyledons and the shoot above them.

The explanations given by many research workers and quoted in a large number of textbooks are based on the study only of serial sections of seedlings in which primary vascular tissue is fully developed. This method of investigation caused the workers involved to conclude that the separate strands of phloem twist and that their orientation is inverted during their passage through the hypocotyl and into that part of the stem above the cotyledons. These conclusions have not been confirmed by more recent ontogenetic studies, which are based on tracing the connection between the simple, axial conducting system of the root on the one hand, and the complex vascular system of the shoot, on the other.

In *Daucus* (Esau, 1940; Foster, 1950), for example, three bundles enter into each cotyledon. The median bundle of these three traces consists of a strand of exarch xylem which is continuous with the protoxylem of the root and is accompanied laterally by two phloem strands. In this strand centripetal differentiation can be followed for some distance into the cotyledon. In contrast with this, each of the lateral cotyledonary traces is collateral with external phloem and endarch xylem on the inside. Throughout the entire length of these bundles the differentiation of the xylem proceeds in a centrifugal direction. These bundles originate from the central portion

of the diarch xylem of the root. Therefore, in the case of *Daucus*, there is a definite continuation, without any inversion, between the primary vascular system of the cotyledons and that of the common axis of the hypocotyl-radicle. In *Daucus* the apical meristem of the epicotyl commences to produce leaf primordia after secondary thickening is initiated in the region of hypocotyl-radicle. The collateral traces of these foliage leaves join with the secondary vascular tissues of the hypocotyl and root.

According to Crooks (1933) the transition between the vascular systems of the stem and root in *Linum* (Fig. 119, nos. 1–6), which also has a diarch root system, is as follows. In the lower part of the hypocotyl the stele is similar to that of the root. A little higher a parenchymatous pith develops in the centre of the stele and at the same time each of the phloem strands divides, resulting in four strands (Fig. 119, no. 4). The development of the metaxylem elements gradually passes to the sides of the protoxylem and so four groups of metaxylem are obtained, each of which is in contact with the inner side of a phloem strand. About half-way along the hypocotyl each of the four metaxylem strands, together with its external accompanying phloem strand, divides into two, so that eight collateral bundles, which constitute cotyledonary traces, are obtained. Still higher, just below the cotyledonary node, the eight traces become arranged in two opposing groups of four (Fig. 119, no. 3 a, a_1 and b, b_1). At the cotyledonary node the two lateral traces of each group (a and a_1) become greatly separated from the inner two and they enter into the cotyledons where they form the two lateral veins. Still higher, the middle two metaxylem strands (b and b_1) again approach one another on the outer side of the protoxylem, so that at the base of the cotyledons the primary xylem is endarch. The two metaxylem strands, which had approached one another, eventually fuse and form the median vein of each of the cotyledons. The phloem groups of the median vein fuse at a higher level within the cotyledon (Fig. 119, no. 2).

The phloem, which is associated with the two leaves of the epicotyl, is already differentiated in the lower part of the hypocotyl at the level where the two strands of the root phloem diverge to form four strands. However, the xylem of the epicotyl develops somewhat later than that of the cotyledons and hypocotyl. The development of the xylem of the collateral bundles of the first foliage leaves above the cotyledonary node is endarch. These bundles develop basipetally into the hypocotyl where they may join with the strands of metaxylem and phloem or where they may terminate blindly within the parenchyma. In the axes of older seedlings (more than 1 week old), the protoxylem is the first to be stretched and crushed. Later, the earliest-formed metaxylem is obliterated in the middle and upper portions of the hypocotyl. Finally, nearly all the primary xylem disappears, but fragments of it may be distinguished in the parenchyma of the transition region, especially in longitudinal sections, for some time or even throughout the life of the plant.

In certain plants, for example *Beta*, in which the root is also diarch, one trace of double nature enters each of the cotyledons. Each of these cotyledonary traces consists of two bundles which are partially fused along the protoxylem. In this case the protoxylem is also brought closer to the centre by the change in the position of differentiation of the metaxylem in the

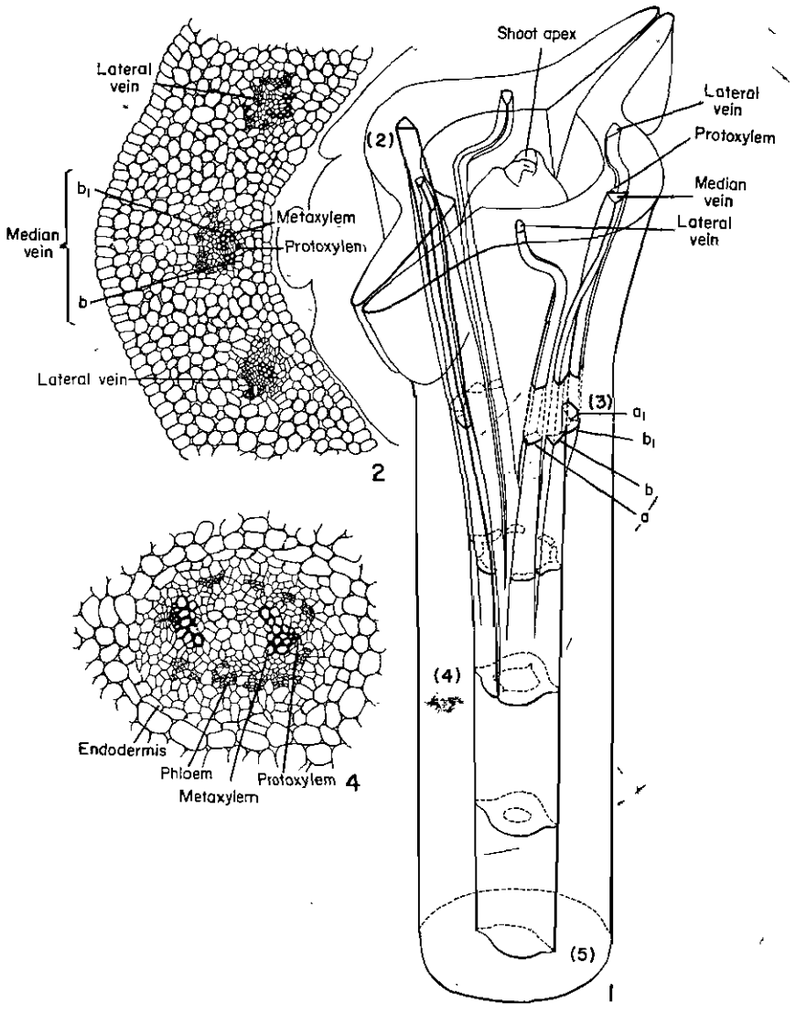

FIG. 119. Transition region in a seedling of *Linum usitatissimum*. 1, Three-dimensional diagram of the hypocotyl and cotyledonary node. 2–5, Portions of cross-sections at various levels of the hypocotyl and of one cotyledon. The numerals in

upper part of the hypocotyl and the bundles become completely collateral and endarch only in the cotyledons (Artschwager, 1926; Hayward, 1938). The double nature of the cotyledonary trace has phylogenetic importance (Bailey, 1956).

In *Medicago sativa* the root is usually triarch. In transition to the hypocotyl one of the xylem strands becomes smaller than the other two. The two large strands become situated one opposite the other as in a diarch arrangement. The small third bundle is at right-angles to the two large ones. Higher up a fourth strand of protoxylem develops opposite the small third one and so the stele becomes tetrarch at the base of the hypocotyl. During this process a fourth strand of phloem is also developed and the phloem strands alternate with the xylem strands. Higher up in the hypocotyl pith is developed. The phloem strands divide so that they number eight; these strands become orientated so as to take up a position almost collateral to the xylem strands. The differentiation of the metaxylem ele-

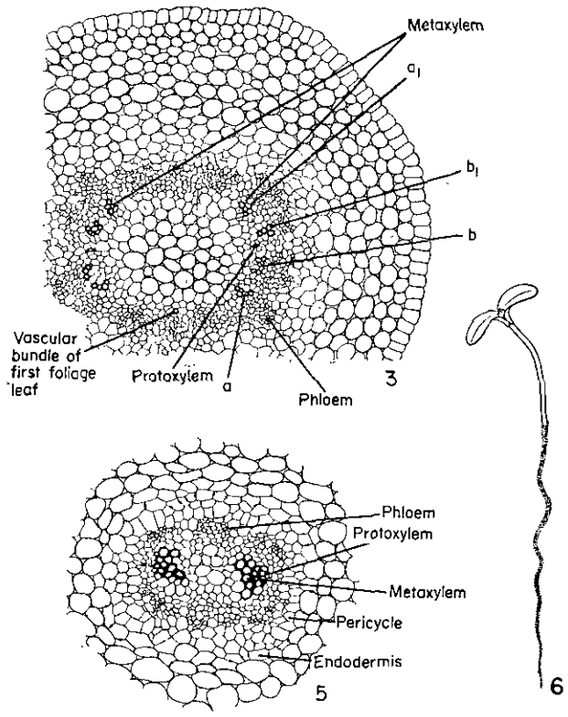

FIG. 119 *(cont.)*

no. 1 indicate the levels at which the cross-sections were made. 6, An entire seedling at the stage of development corresponding to that depicted in the other drawings. For further explanations, see text. (Adapted from Crooks, 1933.)

ments, a short distance below the cotyledonary node, takes place in such a position that two V-shaped groups, as seen in cross-section, are formed. The protoxylem is located in the angle between the two arms of the V. The two triads, i.e. the xylem groups together with their associated phloem, constitute the cotyledonary bundles (Hayward, 1938).

The length of the transition region in dicotyledons differs—in some plants it is short while in others it is long. In some plants the changes in orientation are gradual and continue throughout the entire length of the hypocotyl, while in others these changes are restricted to the upper portion of the hypocotyl alone. In the latter case the hypocotyl is referred to as being of root structure. The transition region is longest in seedlings with subterranean cotyledons (hypogeal germination) as it extends for one or more nodes above the cotyledons.

In monocotyledons the transition between the vascular tissues of the root and stem is affected by the presence of a single cotyledon and by the shortness of the lowermost internodes (Esau, 1953). In many monocotyledons part of the vascular system of the root is connected with the vascular system of the cotyledon, while part is connected with the vascular tissues of the first foliage leaf. In both these cases the connecting vascular strands exhibit features typical of transition. However, in a small number of monocotyledons the transition takes place between the root and cotyledon alone as is common in the dicotyledons (Arber, 1925).

As an example of a transition region in monocotyledons we shall cite that of the seedling of *Triticum* (Fig. 115, no. 3) as described by Boyd and Avery (1936). The polyarch vascular cylinder of the root is connected to that of the leaves by the presence of plate-like vascular tissue which is present below the insertion of the scutellum. This plate is termed the *nodal plate*. Separate bundles arise acropetally from the nodal plate. These bundles are irregularly arranged in the basal portions where they exhibit transitional features. Higher up these bundles continue to branch and produce a cylinder of bundles with endarch xylem and with collateral arrangement of xylem and phloem. This system consists of bundles that enter the scutellum, coleoptile and the first two foliage leaves.

The transition region of the gymnosperms is generally similar to that common in the dicotyledons in which the connection occurs primarily between the root and the cotyledons, but it is more complex than in the dicotyledons because of the increased number of cotyledons (Boureau, 1954).

The complex structure of the transition region between the root and shoot is apparently, as already suggested by Esau (1961), the result of the meeting of influences of two morphogenetic centres—the shoot apex and the root apex. These influences are especially strong in the embryonic stage of the plant where the two centres (apices) are close to each other. The differentiation in that region where the two opposite trends meet should

be intermediate between the two. During the growth of the seedling the two poles move further apart and the influence of each of them on the region near the other is weakened. Accordingly, the extension of the transition region into one or more internodes above the cotyledons in seedlings in which the germination is hypogeal may be explained by the extended influence of the root apex on the basal internodes of the stem as a result of the retarded growth of the hypocotyl in such seedlings.

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SECONDARY BODY OF THE PLANT

GROWTH in thickness that occurs distant from the apices is called *secondary growth*, and the tissues thus produced are termed *secondary tissues*. These tissues constitute the secondary body of the plant. Secondary tissues devel-

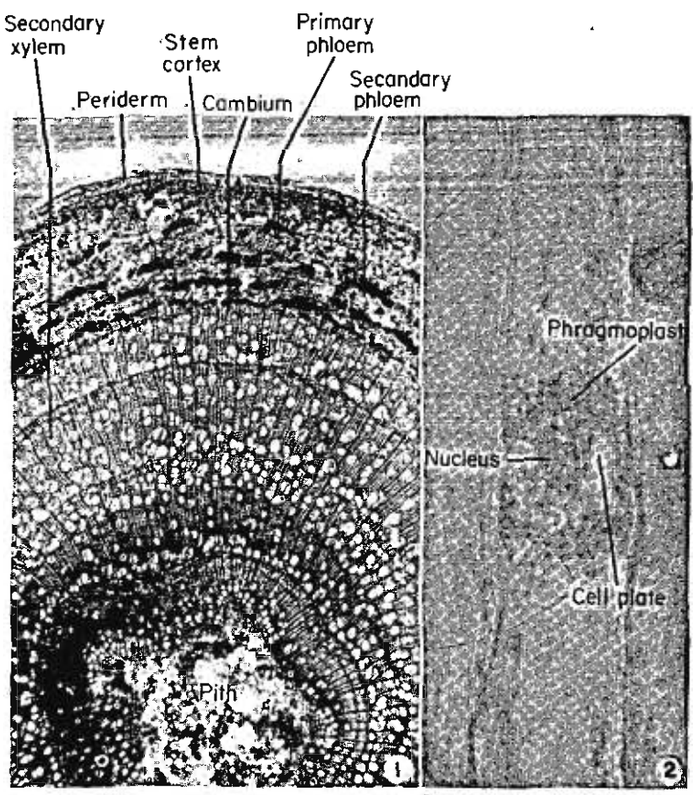

FIG. 120. 1, Portion of a cross-section of a four year-old branch of *Populus alba*. ×40. 2, Portion of a tangential section through the cambium of the stem of *Nicotiana tabacum*, showing the middle portion of a dividing fusiform initial. ×1250.

op from secondary meristems, i.e. from the vascular cambium and the phellogen or cork cambium. Commonly, the main stem, which in certain plants may reach a diameter of some metres, the branches, roots, and often even petioles and the main veins of leaves, consist of secondary tissues (Fig. 120, no.1).

The development of secondary vascular tissues from the cambium is characteristic of the dicotyledons and the gymnosperms. In certain monocotyledons the vascular tissues are also increased after the primary growth is completed, but the cambium of these plants is of a different nature. In the pteridophytes secondary thickening was more common among those species that have become extinct. In the living pteridophytes this feature is rare but occurs, for example, in *Isoetes* and *Botrychium*. Certain monocotyledons, as, for instance, some Palmae, exhibit considerable thickening that is the result of a primary thickening meristem only, but these plants never reach the diameter of old dicotyledonous trees.

CHAPTER 14

VASCULAR CAMBIUM

THE vascular cambium is a lateral meristem that develops either as longitudinal strands or as a hollow cylinder. In the woody angiosperms and gymnosperms the primary tissues of the stem and root exist for only a relatively short period before they become destroyed or obliterated by the development of the secondary vascular tissues which are produced by the cambium. In many herbaceous angiosperms, and also in most of the recent lower vascular plants, cambium is absent or vestigial.

General development and structure of the vascular cambium

In certain plants, including monocotyledons, all the cells of the procambium undergo differentiation into primary vascular tissues. In almost all the dicotyledons and gymnosperms a portion of the procambium remains meristematic even after the completion of primary growth and develops into the cambium of the secondary body. The cambium that arises within the bundles of primary vascular tissue of the stem is called *fascicular cambium* (Fig. 70, nos. 2, 3). The strips of fascicular cambium usually become joined by additional strips of cambium which constitutes the *interfascicular cambium* (Fig. 71). The interfascicular cambium is not a continuation of the procambium but develops from the interfascicular parenchyma. Therefore this part of the cambium constitutes a secondary meristem also from the point of view of its origin. Thus a complete hollow cylinder of cam-

bium is developed which is present throughout the length of the main plant axis and from which there arise narrower cylinders of cambium belonging to the stem and root branches. Sometimes the cambium extends into the leaves. In most dicotyledons and gymnosperms the cambial cylinder develops between the primary xylem and phloem, a position that is retained throughout the life of the plant. From this position the cambium produces the secondary xylem centripetally, and the secondary phloem

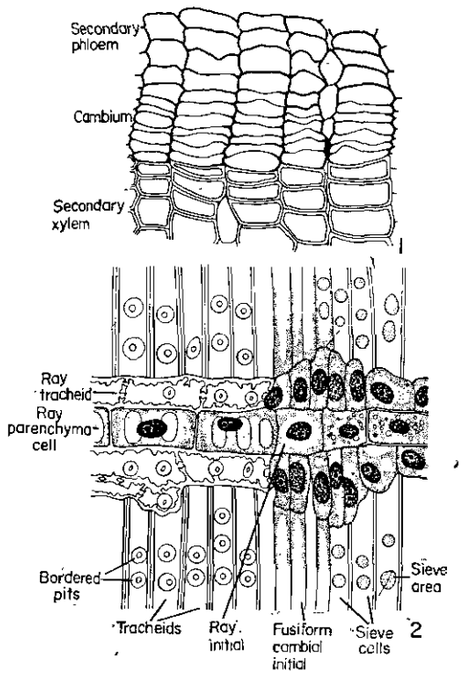

FIG. 121. 1, Portion of a cross-section of a stem of *Pinus* showing the cambial zone and neighbouring tissues. 2, As above but a radial section and showing a vascular ray. (No. 2, adapted from Haberlandt, 1918.)

centrifugally. In certain dicotyledonous plants, e.g. the Chenopodiaceae, the secondary thickening of the axis is anomalous and it is brought about in a manner that differs from that described above.

Among the important investigations of the structure of the cambium and the manner of its cell division are those of Bailey (1920a, b, 1923, 1930), Bannan (1950, 1951a, b), Bannan and Whalley (1950), Newman (1956) and Wilson (1964).

During the growing period the cambial initials together with their immediate derivatives form the *cambial zone*. In a cross-section the cells of the

cambial zone are seen to be arranged in radial rows (Fig. 121, no. 1). The cells on either side of this zone gradually widen until they acquire the shape and features of mature phloem and xylem elements. In the narrow sense of the word the cambium consists only of the single layer of initials, but it is customary to refer to the entire cambial zone by this term as it is difficult, in a single section, to distinguish between the initials and the neighbouring cells that are derived from them. Some authors (Catesson, 1964) doubt the existence of one layer of cambial initials and consider the cells of the whole homogeneous part of the cambial zone to have the properties of initials. When the cambium is active the cambial zone is wide and consists of many cell layers, but when it is dormant the zone is usually reduced to one or a few cell layers only.

In conifers, according to Bannan (1962), the cambial zone in the resting state may consist of five layers, but it is usually two- or three-layered. In the three-layered condition the layer nearest the more or less immature phloem is recognizable as that of the cambial initials and the inner layers constitute the xylem mother cells. In these plants the first divisions, on the renewal of cambial activity, may occur in any of the three layers of the cambial zone, but the usual site of the first divisions is among the xylem mother cells closest to the already differentiated xylem and not, as might be expected, in the cambial initials. The initiation of the divisions closest to the xylem is of interest and may be connected with the supply of water as well as with the presence of growth hormones (Bannan, 1962). According to Evert (1963), in *Pyrus malus* final differentiation of the phloem elements from cells produced in the previous season precedes xylem differentiation by about 6 weeks.

TYPES OF CAMBIAL CELL

There are two basic types of cambial initials.

1. *Fusiform initials* (Fig. 122, nos. 1, 2) which are elongated cells with tapered ends. These cells are very long and in old trunks of *Sequoia sempervirens*, for example, they reach a maximum length of 8·7 mm (Bailey, 1923).

2. *Ray initials* (Fig. 122, nos. 1, 2) which are much smaller cells than those of the above type and which are almost isodiametric.

Both these types of initials are larger in older trunks than in very young ones. The longitudinally orientated elements in an organ, such as the tracheary elements, fibres, xylem and phloem parenchyma and the sieve elements, develop from the fusiform initials. The cells of the vascular rays, which are orientated horizontally in the organ, develop from the ray initials.

One of the interesting features of cambial cells is their intense vacuolation. The walls of these cells possess primary pit-fields with plasmodesmata (Fig. 123, no. 1). The radial walls, especially of the mother cells, are

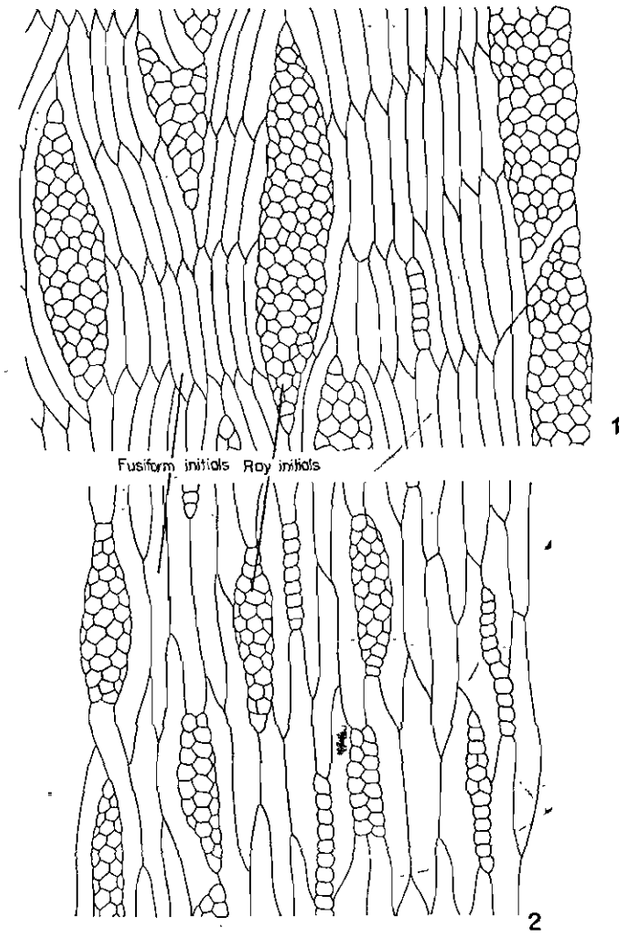

FIG. 122. Tangential sections of different cambial types. 1, Storied cambium of *Robinia*. 2, Non-storied cambium of *Fraxinus*.

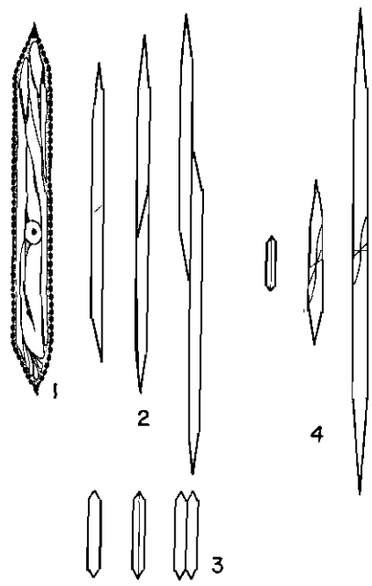

FIG. 123. 1, Diagram of a fusiform initial of the cambium of *Robinia pseudacacia* showing its highly vacuolated protoplast and the presence of numerous primary pit-fields. 2–4, Diagrammatic representation of the anticlinal division of fusiform initials that results in the increase in girth of the cambium. 2, Division of a fusiform initial in non-storied cambium showing the relative position of the daughter cells during their elongation. The plane of the division is diagonal, and the cells come to lie one next to the other as a result of gliding growth. 3, Three stages in the anticlinal division of a fusiform initial in a storied cambium. 4, Three possible orientations of the new wall formed during the anticlinal division of a fusiform initial. From right to left: in conifers, in non-storied dicotyledonous cambium; in storied dicotyledonous cambium. (Adapted from Bailey, 1923, 1930.)

thicker than the tangential ones; this feature is a result of the predominantly periclinal divisions in the cambial cells during which the thickening of the radial walls is continuous.

TYPES OF CAMBIUM

Two types of cambium can be distinguished on the basis of the arrangement of the fusiform cells as seen in tangential section.

1. *Storied or stratified cambium* (Fig. 122, no. 1) in which the fusiform initials are arranged in horizontal rows so that their ends are approximately at the same level. This type of cambium is found in *Tamarix* and *Robinia*, for example.

2. *Non-storied* or *non-stratified cambium* (Fig. 122, no. 2) in which the fusiform initials partially overlap one another and in which they are not arranged in horizontal rows.

The fusiform initials in the second type are longer and this type is the more common. Bailey (1923) saw in the initials of storied cambium a higher phylogenetic stage, and he suggested that they have developed by gradual reduction of the size of the cells and of longitudinal sliding growth.

CELL DIVISION

The cambial initials and the cells that are derived from them but which have not yet undergone differentiation divide periclinally and anticlinally in a longitudinal plane. As a result of the periclinal divisions, which are the more numerous, new cells are added to the secondary phloem and xylem. The derivatives of each initial therefore form radial rows, which can sometimes also be distinguished in the xylem and phloem. Usually, however, this order is lost in the vascular tissues because of the changes in shape that take place during the differentiation and maturation of their cells.

As a result of the secondary thickening, the circumference of the xylem cylinder increases. Together with this the cambium also increases in circumference by the addition of new cells. In storied cambium the addition of new fusiform initials is brought about by longitudinal anticlinal divisions (Fig. 123, no. 3) of the existing initials. In non-storied cambium, on the other hand, the fusiform initials undergo oblique, approaching horizontal, anticlinal divisions, after which each of the new cells elongates at its ends till it is as long as, or even longer than, the cell from which it was derived (Fig. 123, no. 2).

Because of the great length of the fusiform initials the formation of the cell plate during the process of longitudinal division is peculiar to these cells. The cell plate begins to form between the two new nuclei and it spreads slowly. A relatively long period passes before it reaches the end walls. While the cell plate is not complete its free margins are surrounded by phragmoplast (Fig. 120, no. 2; Fig. 124, nos. 1–4).

In the conifers (Bannan, 1962) intensively dividing cambial cells divide once every 4–6 days, whereas apical meristmatic cells divide every 8–18 hr. Possibly, the slower division of the cambial cells is due to the time required for the phragmoplasts to reach the ends of the elongated cells, which may be up to a few millimetres long. Most divisions, as seen in radial longitudinal sections, take place among the xylem mother cells. The rate of division in the cambial initials and the phloem mother cells is lower than in the xylem mother cells. The relative rates of xylem and phloem formation have been found to change during the growing season only in some plants. According to Bannan (1950, 1951a, b), in the conifers

there are two processes that take place during the enlargement of the cambial cylinder. Firstly, nearly all the new ray initials develop from special, transverse divisions of fusiform cells. Secondly, single initials are continually lost from the cambium and are replaced by new ones. Many of the fusiform initials that are about to be lost shorten before they are finally obliterated.

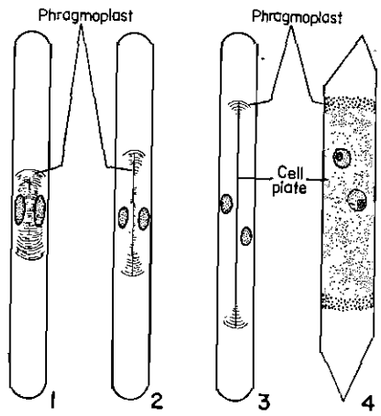

FIG. 124. Diagrams showing various stages in the division of a fusiform initial of *Robinia pseudacacia*. 1–3, Dividing cells as seen in radial section. 4, As seen in tangential section. (Adapted from Bailey, 1920c.)

Seasonal activity of Cambium

There are plants whose cambium is active throughout the entire life of the plant, i.e., the cambial cells divide continuously and the resulting cells undergo gradual differentiation to form the xylem and phloem elements. This type of activity is usually found in plants growing in tropical regions. Contrary to this, in plants whose origin is in the temperate regions, the cambium ceases its activity with the onset of unfavourable conditions, usually the autumn, and it enters a dormant state which may last from the end of summer till the following spring. In spring the cambium again becomes active. From an anatomical point of view the commencement of the cambial activity consists of two stages: (1) the cambial cells become wider radially; and (2) the cells begin to divide as described above. With the enlargement of the cambial cells their radial walls usually become weakened, so that in this stage the bark of the stems and roots may easily be peeled. In later stages this easy separation of the bark from the xylem is also possible because of the increase in number of cells in the cambial zone as a result of the cell divisions. The separation principally occurs in the region of the young xylem cells which have already reached their maximum diameter, but which still have thin primary walls.

Various methods are used to determine cambial activity. The ease by which the bark may be peeled is often used as an indication of cambial activity. A second method is based on the anatomical examination of cross-sections cut in the region of the cambium and the tissues adjacent to it. In this method the number of cell layers of not yet fully differentiated xylem elements is taken as an indication of the rate of cambial activity. Recently a new method has been developed by which both the rates of cell division and of cell differentiation can be precisely determined (Waisel and Fahn, 1965a). This method involves the application of radioactive carbon to photosynthesizing plants. If the cambium is active the radioactive carbon is incorporated in the newly formed cell walls where it can easily be detected by autoradiographic techniques.

As has already been mentioned, there are plants in which the cambium is active throughout the year and those in which there is a break, which may be as long as 8 months in duration in the cambial activity. In the Mediterranean and desert regions of Israel it is possible to find both the above two as well as intermediate types (Oppenheimer, 1945; Fahn, 1953, 1955, 1958a, b, 1959a, b, 1962; Fahn and Sarnat, 1963). In these regions the range of temperature is such that the cambium may remain active throughout the year if such activity is in accordance with the hereditary characteristics of the plant. In arid regions, such as these, however, the amount of available water in the soil is an important factor in the control of cambial activity, and, of course, the general ability to grow depends on this factor. It is of interest to note that in certain plants, e.g. *Tamarix articulata*, *Acacia raddiana* and *A. tortilis*, which grow in the desert regions of Israel and whose roots reach those levels that contain a certain amount of moisture even at the end of the dry summer, the cambium is active throughout the year. From the point of view of cambial activity the trees and shrubs growing in Israel may be divided into the following five types.

1. Woody plants, such as *Retama raetam* Webb., *Artemisia monosperma* Del., *Zygophyllum dumosum* Boiss. and *Reaumuria palaestina* Boiss., which all exhibit more or less distinct growth rings, the development of which commences in the early winter months, i.e. between November and January. The cambium in these species is dormant for a fairly long period.

2. Trees and shrubs such as three *Quercus* species, three *Pistacia* species, *Ceratonia siliqua* L., *Tamarix jordanis* Boiss. var. *negevensis* Zoh., *T. gallica* L. var. *maris-mortui* Zoh., and *Calligonum comosum* L'Her. which all exhibit more or less distinct growth rings, the development of which commences in the period March to May, i.e. in the spring. Some of the plants of this group have a marked dormant period, while in others, such as *Ceratonia* and the two *Tamarix* species, the cambium is inactive for a very short period only, and may even be active throughout the year. In the

latter case only the seasons of early and late wood production can be determined.

3. Shrubs, such as *Anabasis articulata* Moq. and *Salsola rosmarinus* Solms-Laub., which are intermediate between the first two groups in that the commencement of the growth-ring production is in February.

4. Trees, such as *Eucalyptus camaldulensis* Dehn. and *Tamarix aphylla* Karst., in which the formation of the early wood starts in September (August), i.e. toward the end of the dry summer season. In *Eucalyptus* the late wood, which consists of one or two bands of flattened fibres two or three layers thick, is produced during the spring or in early summer, and the cambium is inactive or almost so during July–August. In some specimens of *Tamarix aphylla* commencement of growth-ring production was found to be in August–September, while in other specimens two such periods were seen – one in the late summer and one at the end of February – resulting in the production of two growth rings annually.

5. Trees and shrubs, such as *Acacia tortilis* Hayne, *A. raddiana* Savi, *A. cyanophylla* Lindl. and *Thymelaea hirsuta* Endl., in which there are no growth rings and in which the same type of wood is produced throughout the year.

In *Eucalyptus camaldulensis* the annual growth ring was seen to be produced in September which coincides with the spring of Australia, where this plant is indigenous. Therefore it is seen that the endogenous growth rhythm persists in the trunk of *Eucalyptus* species and that it withstands the influence of external factors in a new and different environment. In the case of Israel this is probably possible because of the mildness of the winters. This feature of the growth rhythm is, however, confined to evergreens, as in deciduous plants the endogenous rhythm of cambial activity may become suppressed under the influence of sudden changes in climate that bring about leaf fall and bud burst. In the grapevine a second bud burst, which was accompanied by the formation of a second growth ring, could be artificially induced by defoliation (Bernstein and Fahn, 1960).

From the behaviour of tropical woody species and of *Eucalyptus* introduced into an area with a mild climate, it appears that the annual rhythm of growth-ring production, at least in evergreens, may be considered as a conservative character. Therefore it may be that the plants of the above-described types are of different geographic origin. The first group, in which the growth-ring production commences between November and January, i.e. at the beginning of the wet winter, and in which the cambium is active during that period and dormant during the dry season, appears to be the indigenous type, and it is the best suited to the area under discussion.

COMMENCEMENT OF CAMBIAL ACTIVITY AND FACTORS INFLUENCING IT

The relationship between the cambial activity and the activity of the vegetative buds differs in different species. The activity of the cambium usually starts below the sprouting buds from where it spreads downwards. The velocity of this spread also differs. In *Acer* it was found to be rather slow (Cockerham, 1930) while in various conifers, in some ring-porous dicotyledons (Priestley, 1930; Wareing, 1951) and in some evergreens (Fahn, 1953) the downward spread of the cambial activity is very rapid. For instance, in the Mediterranean region of Israel the time lag between bud sprouting and the activation of the cambium is 2–4 weeks in some deciduous species, while in evergreens there is no such lag and the two processes take place simultaneously (Fahn, 1953).

The stimulus for the reactivation of the cambium is, apparently, a certain level or combination of growth-regulating substances (Gouwentak, 1941). The close relation of cambial and bud activity led Avery *et al.* (1937) to conclude that these substances, which are produced by the buds, flow downwards from them along the axis where activity is thus induced. However, in most plants a certain period of dormancy must be completed before the cambium can be reactivated by known treatments, such as the application of growth regulators (Gouwentak and Mass, 1940; Gouwentak, 1941) and increased day length. Thus, the application of such treatments will induce activity only after a certain unknown factor or factors, which cause dormancy, have been eliminated.

According to Wareing (1958) two main groups of regulators, i.e. gibberellins and auxins, have been shown to affect cambial activity. Under the influence of gibberellin rapid cell divisions, which are not followed by differentiation, are induced in the cambium. Auxins, on the other hand, cause rapid cell differentiation. The simultaneous effect of the above two groups of substances seems to result in the appearance of normal cambial activity.

Very little is as yet known about the factors that cause the cessation of cambial activity. Wareing (1951) and Wareing and Roberts (1956) have stressed the role of photoperiodism in the activity of the cambium. These investigators showed that in juvenile plants of *Robinia pseudacacia* and *Pinus sylvestris* cambial dormancy can be induced by the application of short day conditions and that the cambium can be reactivated by long day conditions. However, other external factors, such as temperature (Waisel and Fahn, 1965b), as well as internal ones, especially in adult plants, seem to play a major role in the control of the rhythm of cambial activity.

Part played by cambium in healing of wounds

One of the important functions of the cambium is to form *callus* or *wound tissue* over wounds. This tissue consists of masses of soft parenchyma tissue which are rapidly formed on or below the damaged surface of stems and roots. Callus may be formed by the division of parenchyma cells of the phloem, cortex and vascular rays, but it is mostly formed by the cambium. The outer cells of the parenchymatous masses become suberized or a periderm develops in them (Chapter 17). Below this protective layer a reorganized cambium produces new vascular tissues.

Callus is also developed, at the beginning of the growth season, on the circumference of wounds caused by pruning. With the continued production, by the cambium, of secondary xylem in the undamaged area around the scar, and because of the eventual fusion of the cambial layers, the wound becomes completely covered. The production of the secondary wood continues so that the layer covering the wound is continually thickened.

If the cambium is damaged during the growing season it may be reformed from the immature xylem cells below it if these cells are protected from drying-out immediately after the wound is formed. Sometimes in ringing experiments it is difficult to prevent the formation of new cambium even if the ringed surface is scratched with a knife, as the living immature xylem cells below it produce callus tissue in which the new cambium is developed.

Part played by cambium in grafting

The important process of grafting is based on the ability of the cambium to form callus in the stock and scion, and to fuse so as to form a continuous layer at the junction of the stock and scion. This cambium develops, after fusion, normal vascular tissues (Mendel, 1936; Roberts, 1949; Mosse, 1953; Buck, 1954). In cases where the stock and scion are incompatible, their cambia do not fuse and normal phloem and xylem is not produced. Instead, parenchymatous masses are formed which result in a weak union and which only enable slow conduction (Roberts, 1949; Mosse and Herrero, 1951; Herrero, 1951; Mosse, 1955).

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CHAPTER 15

SECONDARY XYLEM

THE cambium, which is described in the preceding chapter, produces, towards the centre of the stem and root, secondary xylem which comprises various elements—tracheids, vessel members, different types of fibres, parenchyma cells, xylem ray cells, and sometimes secretory cells. The occurrence and the arrangement of these elements varies in different groups of plants. The quantitative differences in the number of cells, as well as in the size of the elements that exist between the species of a single genus, make it possible to identify the plant by its secondary xylem alone.

Usually it is difficult to distinguish clearly between the primary and secondary xylem. The best distinguishing feature between these two tissues is the length of the tracheary elements (Bailey, 1944). The first-formed tracheary elements of secondary xylem are much shorter than the tracheary elements of primary xylem; they are even shorter than the pitted tracheary elements of primary xylem which are themselves usually shorter than the spirally thickened elements. This feature may be the result of stretching, which takes place during the development of the primary xylem elements, but not during that of elements formed by the cambium. Also it is possible that, prior to the differentiation of the cambium from the procambium, the cells of the latter divide transversely.

The structure, ontogeny and phylogeny of the various xylem elements, both primary and secondary, have already been dealt with in Chapters 6 and 7. This chapter will mainly discuss the arrangement of the elements in the secondary xylem.

BASIC STRUCTURE OF SECONDARY XYLEM

The most distinctive feature characterizing the secondary xylem is the existence of two systems of elements which differ in the orientation of their longitudinal axes—one system is vertical and the other horizontal. The horizontal system comprises the xylem rays (Fig. 126; Fig. 132), and the vertical or axial system, the tracheary elements, fibres and wood parenchyma. The living cells of the rays and of the axial system are usually interconnected, so that it is possible to speak of a continuous system of living cells. This system is generally connected with the living cells of the pith, phloem and cortex.

WOOD PARENCHYMA

Two types of parenchyma are found in the secondary xylem—the *axial parenchyma* and the *ray parenchyma* (Fig. 132). The ray parenchyma cells originate from special, relatively short cambial initials, while the cells of the axial parenchyma develop from fusiform initials. The cells of the axial parenchyma may be as long as the fusiform initials from which they are derived or much shorter as a result of transverse division prior to differentiation. The shorter axial parenchyma cells are the more common.

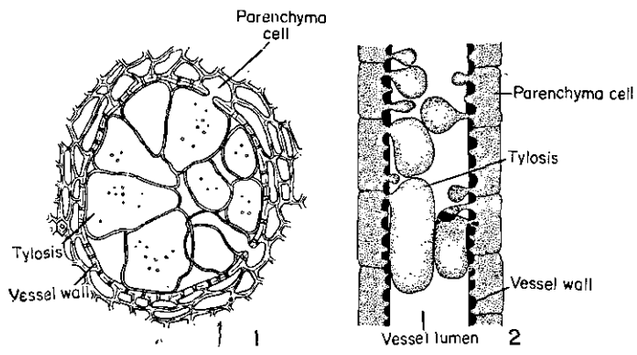


FIG. 125. 1, Cross-section of a vessel of *Robinia pseudacacia* showing tyloses. 2, Longitudinal section of a vessel of *Vitis vinifera* showing the development of tyloses from the neighbouring parenchyma cells. (No. 1, adapted from Strasburger.)

The ray-parenchyma cells may be variously shaped, but the following two forms are the most common: that in which the longest axis of the cells is radial, and that in which it is vertical. All ray parenchyma cells may have secondary walls, or only primary walls may be developed. Where secondary walls are developed the pit-pairs may be simple, half-bordered and sometimes even bordered.

The parenchyma of the xylem serves to store reserve materials, such as starch and oil. Tannins, crystals and other substances are also frequently found in many of these cells. Sometimes the parenchyma cells containing crystals divide so that chambers, each containing one crystal, are formed (Chattaway, 1955, 1956).

In many plants the cells of both types of wood parenchyma form protuberances which penetrate through the pits into the vessels after they become inactive, or into the vessels of xylem tissue that has been injured. These outgrowths are termed *tyloses* (singular: *tylosis*) (Fig. 125, nos. 1, 2;

Fig. 129, nos. 1, 2). The nucleus and part of the cytoplasm of the parenchyma cells, from which the tylosis is formed, enter the tylosis. Tyloses may divide.

RAYS, CELL ARRANGEMENT, HEARTWOOD AND SAPWOOD

The number of xylem rays in a trunk increases with the increase in its girth. The length, width and height of each ray can be measured. The length of the ray is determined in cross-sections of the wood. The width of the ray is measured in tangential sections and it is usually expressed as the maximal number of cells in a horizontal direction. The height of the ray, parallel to the longitudinal axis of the stem or root, is also measured from tangential sections and it is usually expressed in one of two ways – if it is not very large, in the number of cells, and if it is very large, in microns or millimetres. The dimensions of the rays vary in the different plants and sometimes even in the same plant. When the ray is one cell wide, it is said to be a *uniseriate ray* (Fig. 127, no. 4); when two cells wide, *biseriate* and when more than two cells wide, *multiseriate* (Fig. 130, no. 1). In a tangential section a multiseriate ray is seen to become narrow towards both its upper and lower edges, where it is usually uniseriate.

In species that have a storied cambium (see Chapter 14) a similar arrangement may exist in the xylem (Fig. 130, no. 1). Sometimes the storied arrangement becomes indistinct because of the intrusive growth of the ends of the developing fibres and tracheids. The blurring of the arrangement occurs to different extents so that it is possible to distinguish different degrees of storied arrangement from that where the fibres, tracheids and axial parenchyma cells are equal in length and are arranged in horizontal rows, to that in which arrangement of the xylem elements is similar to that developed from a non-storied cambium. In storied xylem the vessel members are usually short. Phylogenetically the storied arrangement is thought to be the more advanced.

The outer part of the secondary xylem contains living cells and at least part of it is active in the transport of water. The outer part is termed the *sapwood* or *alburnum*. In most trees the inner portion of the secondary xylem completely ceases to conduct water and living cells in it die. This is accompanied by the disintegration of the protoplast, the loss of the cell sap and the removal of reserve materials from cells that stored them. In those species in which tyloses are a characteristic feature of the wood the vessels in this inner portion become totally blocked, at this stage, by the formation of tyloses. The cell walls of the parenchyma cells which were little lignified may become more heavily lignified. Certain substances, such as oils, gums, resins, tannins, coloured substances and aromatic compounds, develop in the cells, or are accumulated in them. In the gymnosperms the flexible pit membrane becomes rigid and fixed in such a position that the torus

closes the pit aperture. Secondary xylem that has undergone such changes is termed *heartwood* or *duramen* (Fig. 131, no. 1). The above-mentioned changes make the heartwood more resistant to decay. The accumulation of coloured substances in this part of the xylem makes it easily recognizable from the sapwood. Heartwood may sometimes be developed as the result of pathological conditions.

The quantitative relation between the amount of heart- and sapwood, and the degree of difference between them varies greatly in the different species, and the differences are influenced by the conditions under which the plants are grown. In certain trees, e.g. *Populus*, *Salix*, and *Abies*, no distinct heartwood is developed. In trees such as *Robinia* and *Morus* the sapwood is very narrow, while in *Acer*, *Fraxinus* and *Tamarix* the sapwood is wide.

There are fundamental differences in the histological structure of the wood of dicotyledons and that of gymnosperms, and especially of that of the conifers. In the timber trade the wood of dicotyledons is known as *hardwood* and that of gymnosperms as *softwood*. These terms do not accurately express the degree of hardness, as in both groups wood with both hard and soft structure can be found.

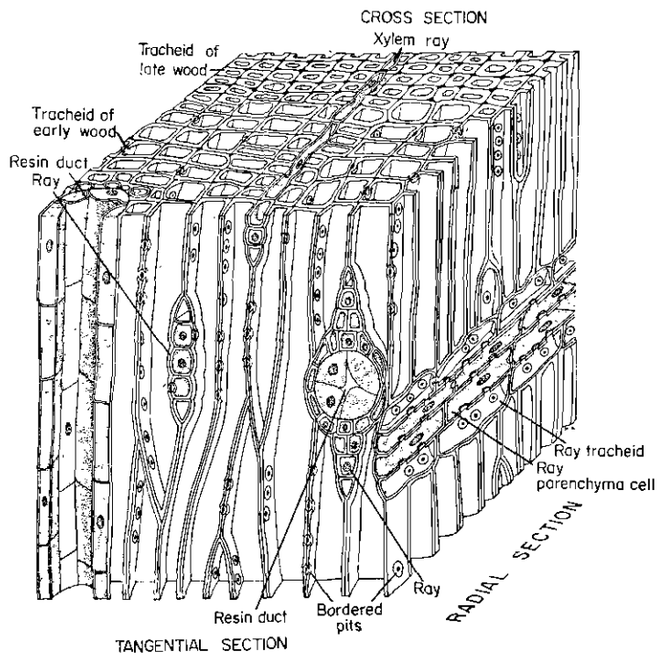


FIG. 126. Three-dimensional diagram of a cube of secondary xylem of *Pinus halepensis*.

Secondary xylem of Gymnospermae

The structure of the secondary xylem of the gymnosperms (Fig. 126) is simpler and more homogeneous than that of the angiosperms. The principal differences are the absence of vessels in the wood of gymnosperms (with the exception of the Gnetales) and their presence in the angiosperms, and the relatively small amount of wood parenchyma, especially axial parenchyma, in the gymnosperms.

THE VERTICAL SYSTEM

In most gymnosperms, the tracheary elements of the vertical system are, as has already been mentioned, tracheids. However, the tracheids of the late wood (i.e. those formed at the end of the growing season) develop relatively thick walls and their pits have small pit chambers and long canals. Because of this structure these tracheids may be termed fibre-tracheids. Libriform fibres are not found in the secondary xylem of gymnosperms. The xylem formed at the end of the growing season appears darker because of the special structure of its tracheids, and so growth rings in conifers are easily distinguishable.

The tracheids (and the fibre-tracheids) are from 0·5 mm to 11 mm long. Because of this great length each tracheid comes into contact with one ray or more. The tracheids overlap one another with flat, chisel-shaped ends. Neighbouring tracheids are joined by bordered pits which may be arranged in a single longitudinal row or in a few rows. In the latter case the pitting may be opposite or alternate. From various investigations it has been shown that the number of pits per tracheid may be from 50 to 300.

The size of the pits, the shape of the pit border and of the pit aperture, vary very greatly and therefore these features are important in the identification of gymnosperm wood. The pits are more numerous at the ends of the tracheids where they overlap one another. Usually the pits are present only on the radial walls of the tracheids, but in the tracheids of the late wood pits are also present on the tangential walls. Pits with tori are found in *Ginkgo*, the Gnetales and most of the Coniferales. In a microscopic radial longitudinal section of the wood of many gymnosperm species transversely orientated thickenings of the wall can be observed above and below the pits (Fig. 133, no. 4). These are thickenings of the middle lamella and the primary walls, and they are termed *crassulae* (see also Chapter 2).

Another feature of gymnosperm wood is the occurrence of *trabeculae* in the tracheids. Trabeculae are rod-shaped outgrowths of the tangential cell walls which grow across the cell lumen so as to connect the tangential walls. Tracheids containing trabeculae are usually arranged in long radial rows.

In some conifers spiral thickenings have been observed on the internal wall surface of the pitted tracheids.

When axial parenchyma is present in the wood of conifers it is usually arranged in strips that are equally distributed throughout the secondary xylem. In certain conifers, e.g. *Araucaria* and *Taxus*, axial parenchyma is completely absent. In *Pinus* axial parenchyma is present only in connection with the resin ducts (Fig. 126).

RAYS

The rays in gymnosperms may comprise parenchyma cells only, i.e. *homocellular rays*, or parenchyma cells and tracheids, i.e. *heterocellular rays* (Fig. 126). The ray tracheids are distinguished from the ray parenchyma mainly by the presence of bordered pits and by the absence of a protoplast. The ray parenchyma cells contain living protoplasts in the sapwood, and generally in the heartwood, darkly coloured resins. The walls of the parenchyma cells may be primary only (e.g. in the Taxodiaceae, Araucariaceae, Taxaceae and Cupressaceae) or secondary as well (e.g. in most species of the Pinaceae).

The ray tracheids all have lignified secondary walls. In certain conifers these cells have very thick walls with tooth-like or band-like thickenings which project into the cell lumen (Fig. 121, no. 2). The ray tracheids occur singly or in rows. They may be at the upper or lower edges of the ray, or they may be scattered among the ray parenchyma cells.

In the large majority of gymnosperms the rays are uniseriate and they are usually from one to twenty cells high, but they may be as high as sixty cells. If a resin duct passes through a ray it passes through the centre of the ray, which becomes more than one cell wide in that position.

Where the vertical tracheids come in contact with ray parenchyma cells the pit-pairs are usually half-bordered, i.e. the bordered pit is situated on the side of the tracheid and the simple pit on the side of the parenchyma cell. This area of contact between a ray parenchyma cell and a single vertical tracheid is termed a *cross-field*. The type of pits, their number and distribution in the cross-field are important features in the identification of gymnosperm wood (Fig. 127, no. 3).

RESIN DUCTS

Resin ducts are developed in the vertical or both vertical and horizontal systems of a large number of gymnosperms. The ducts develop schizogenously between resin-producing parenchyma cells which then form the epithelium of the duct. Sometimes a resin duct may become blocked by

the enlargement of the epithelial cells; such structures are termed *tylosoids*. Differences exist in the thickness and lignification of the cell wall of the epithelial cells in the various conifer genera. In those genera, where the

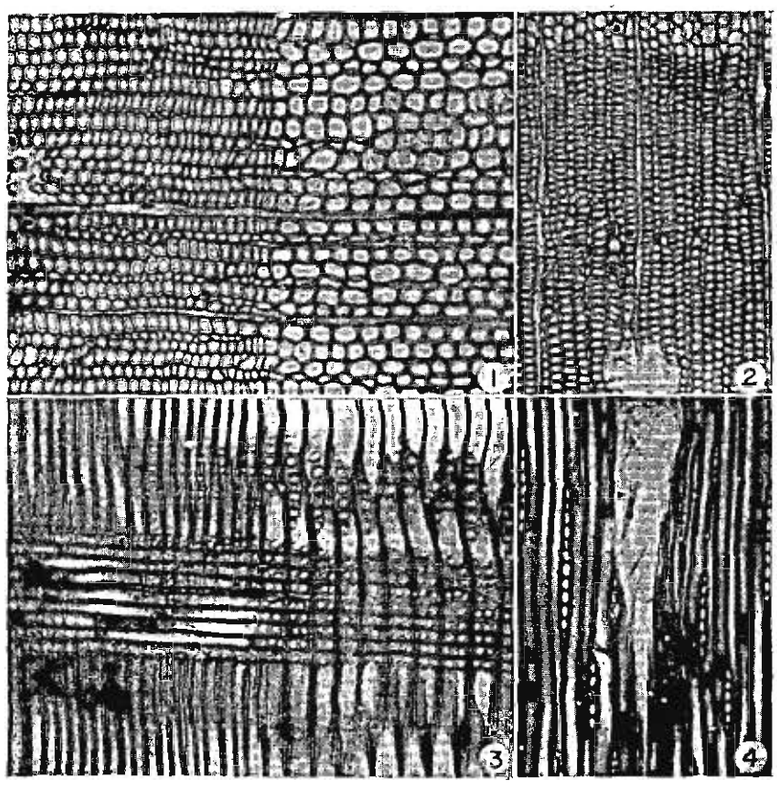


FIG. 127. Micrographs of the secondary xylem of *Pinus halepensis* sectioned in different planes. 1, Cross-section showing the border between the two growth rings. ×95. 2, Cross-section showing a resin duct. ×70. 3 Radial section of a portion between the two growth rings. ×95. 4, Tangential section of a portion incorporating a resin duct. ×95.

resin-secreting cells have thick, lignified walls and in which these cells die after one season, relatively little resin is produced. In those plants where the epithelial cells are thin walled and function during several seasons a large amount of resin is produced. Resin ducts, the epithelial cells of which have lignified walls, occur in *Abies* and *Cedrus*, for example, while in *Pinus* the secretory cells are thin walled and not lignified (Fig. 127, nos. 2, 4; Fig. 128, no. 2; Fig. 126).

It is thought that in the secondary xylem of conifers resin ducts are produced as a result of injuries, such as wounding, pressure and frost, among others. In certain conifers such as *Cupressus*, for example (Fig. 128, no.

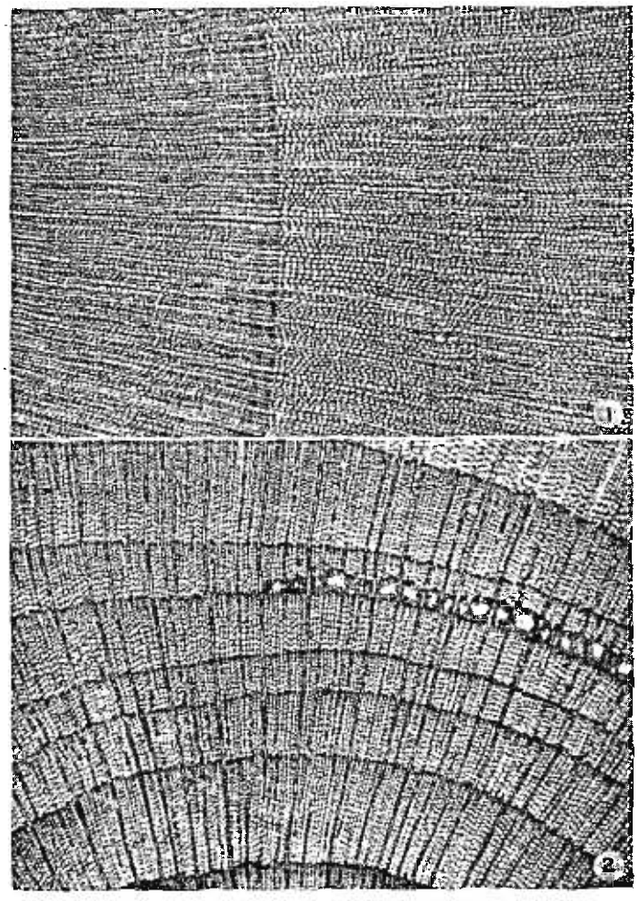


FIG. 128. 1, Cross-section of the secondary xylem of *Cupressus sempervirens*. ×40. 2, Cross-section of the secondary xylem of *Cedrus libani* in which resin ducts, developed as a result of wounding, can be seen. ×36.

1), resin ducts are never developed in the secondary xylem. The location of the resin ducts, when formed in the xylem, depends on the type of injury and on the plant species. For instance, an open wound results in the formation of dense or scanty tangential groups of resin ducts around the

wound. Injuries resulting from pressure or any other factor that acts on a relatively large area results in the formation of scattered ducts. The extent of this scattering depends on the genus: in *Pinus*, for example, the ducts are more scattered than in *Abies* or *Cedrus*. In the last two the ducts are short

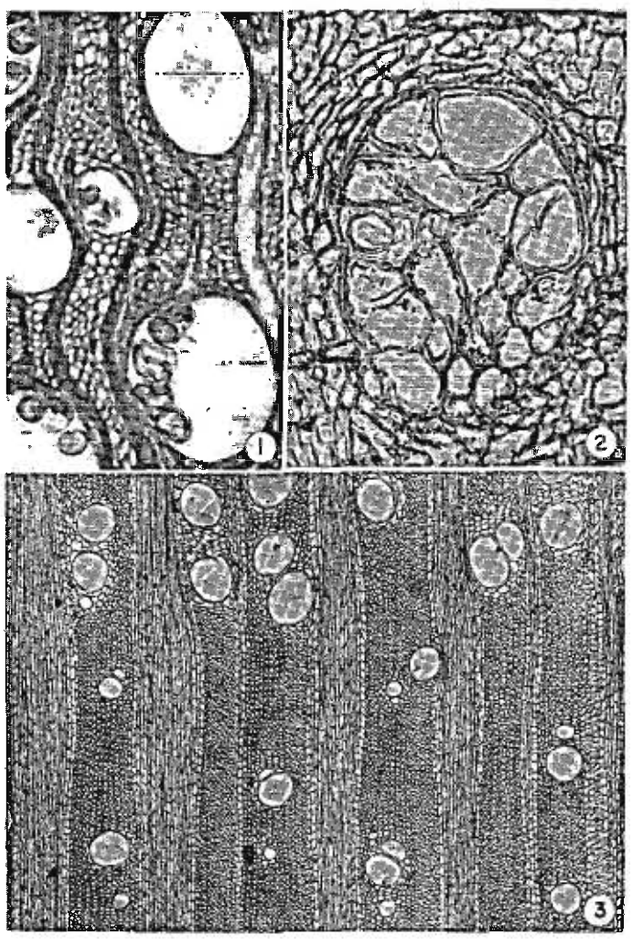


FIG. 129. 1, Micrograph of a portion of a cross-section of the secondary xylem of the root of *Eucalyptus camaldulensis* showing the beginning of the development of tyloses in the vessels. ×120. 2, Cross-section of the secondary xylem of the stem of *Quercus ithaburensis* showing a vessel blocked by fully developed tyloses. ×210. 3, Cross-section of the secondary xylem of the stem of *Tamarix aphylla* showing the expansion of the rays between adjacent growth rings and the vasicentric parenchyma. ×35.

and branched. In *Pinus* the ducts which develop a great distance from the centre of the injury are very long and are not arranged in groups, but are scattered to a great extent. From the results of experiments it has been

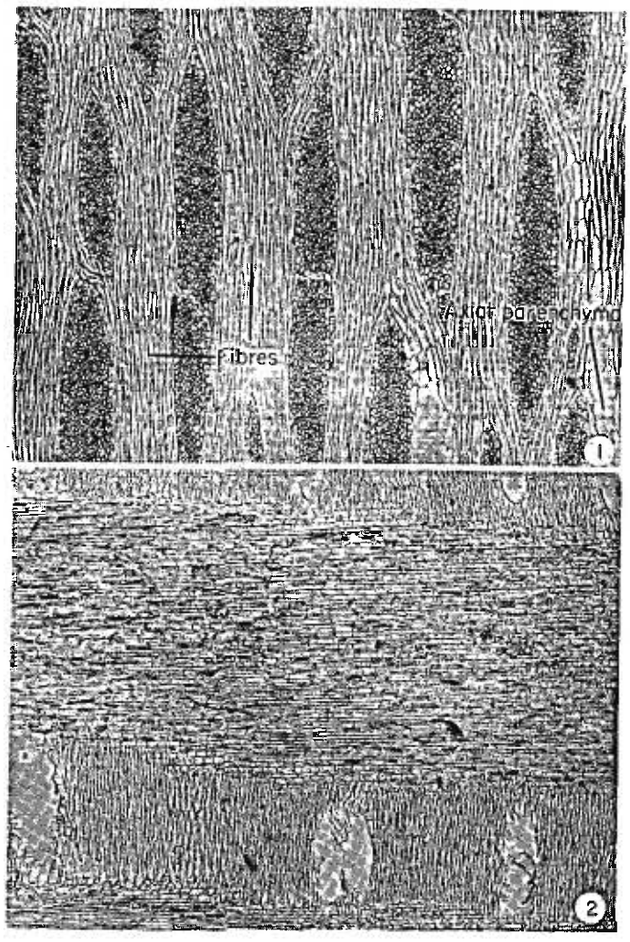


FIG. 130. Secondary xylem of the stem of *Tamarix aphylla*. 1, Tangential section. ×35. 2, Radial section showing heterogeneous rays. ×35.

shown that the largest number of resin ducts is produced when the cambium of the injured branches is intensively active (Bannan, 1933, 1934, 1936; Messeri, 1959 and Spurr, 1950).

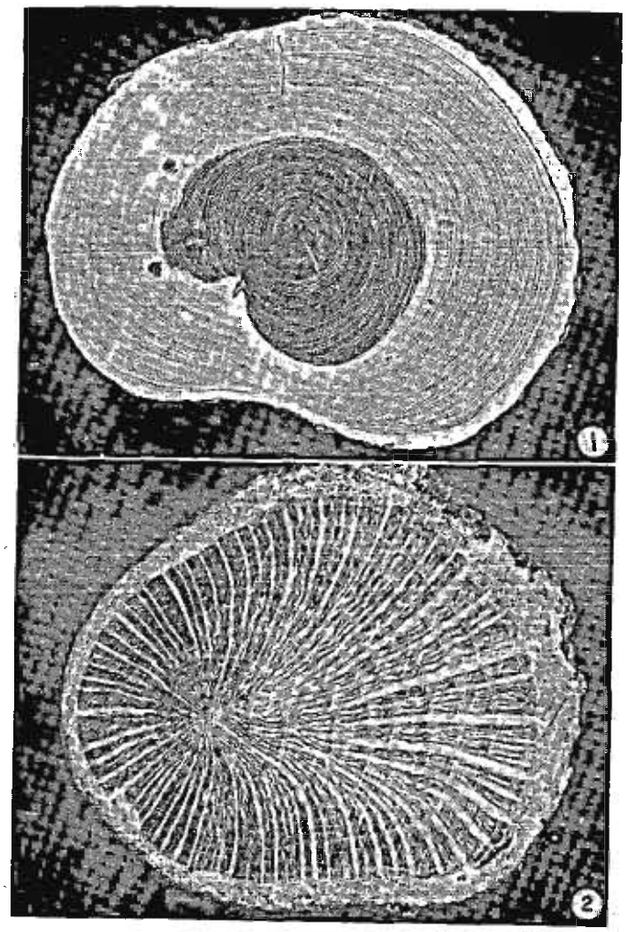


FIG. 131. 1 An entire cross-section of a branch of *Acacia raddiana* in which, from the outside inwards, the bark, sapwood and dark heartwood can be distinguished. ×0·5. 2 As above, but of *Quercus boissieri* in which the very broad rays and eccentric growth rings are readily distinguished. ×1½.

Secondary xylem of Dicotyledonae

The secondary xylem of dicotyledons (Fig. 132) is more complex than that of the gymnosperms. Dicotyledonous wood comprises elements that vary in size, shape, type and arrangement. In the secondary xylem of *Quercus*, for example, vessel members, tracheids, fibre-tracheids, libriform

fibres, gelatinous fibres (Chapter 6), wood-parenchyma and rays of different sizes, are found. However, there are some dicotyledonous trees in which the wood is comprised of a smaller number of element types. For

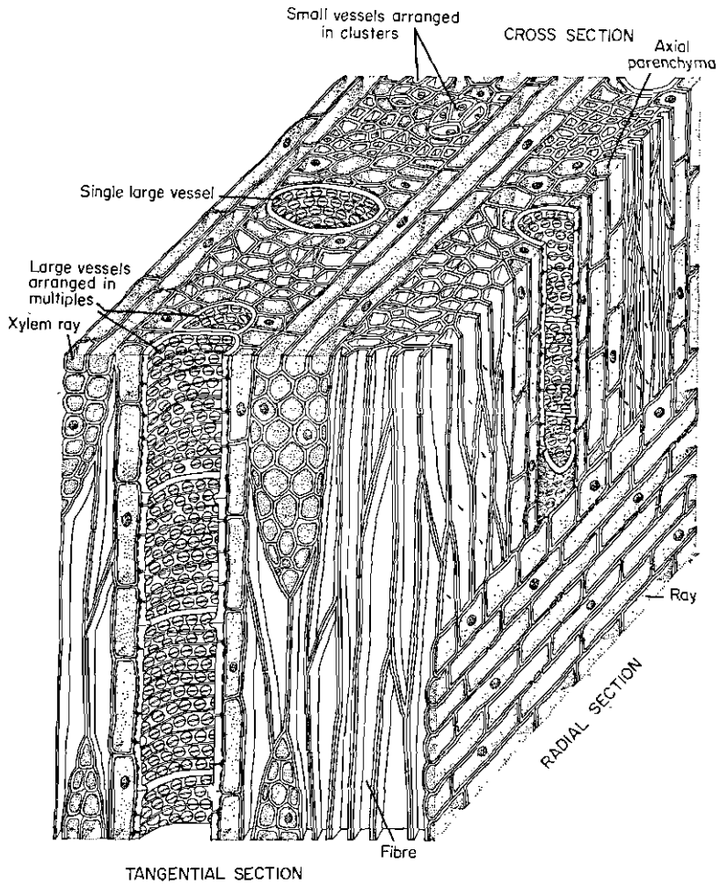


FIG. 132. Three-dimensional diagram of a cube of secondary xylem of *Cercis siliquastrum*.

instance, in many species of the Juglandaceae, apart from vessel members and parenchyma cells, only fibre-tracheids are found in the wood.

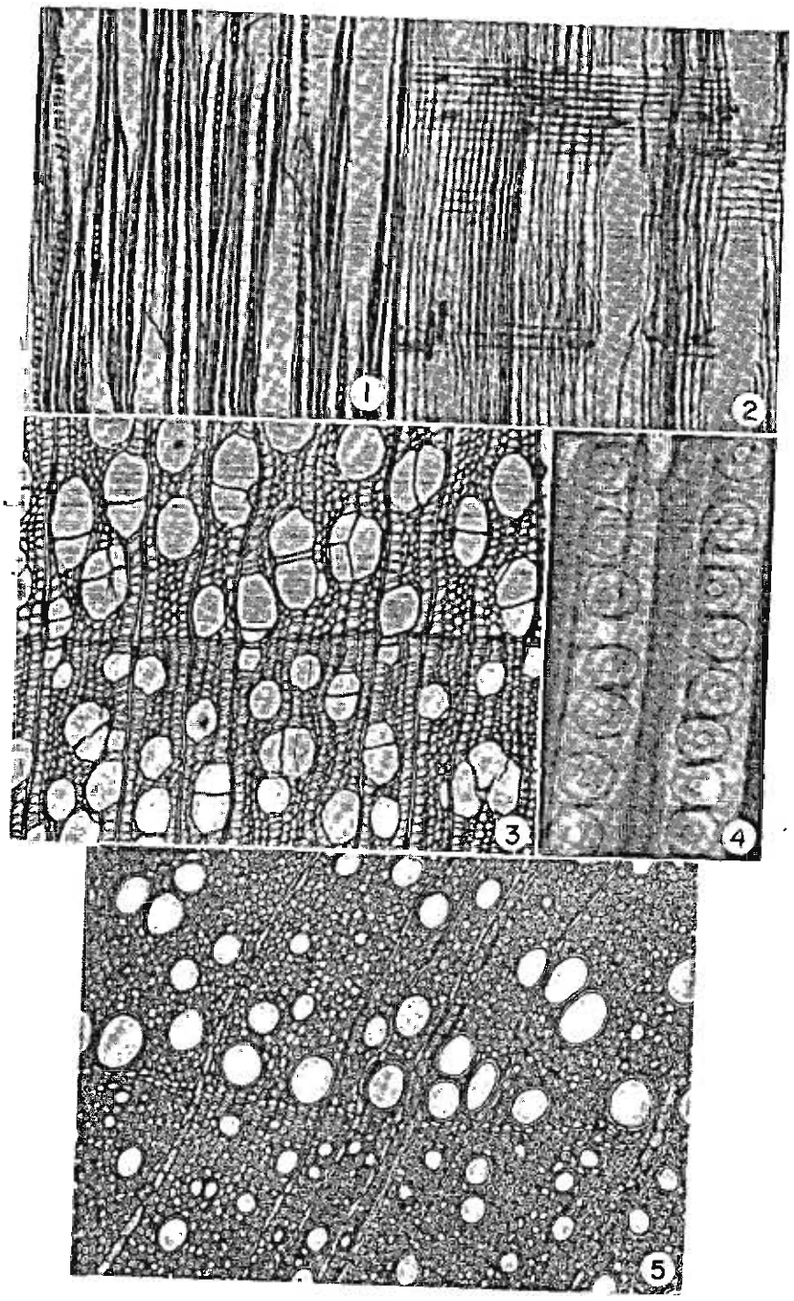
In trees of tropical origin, growth rings are not usually distinguishable, while in trees of temperate origin growth rings can usually be distinguished in the secondary xylem. These growth rings are generally annual, that is, one such ring is produced each year; but there are trees, for instance,

certain specimens of *Tamarix aphylla* (Fahn, 1958), in which two rings are produced in a single year. The growth rings are obvious because of the seasonal differences in amount and shape of certain of the cells developing from the cambium. The cells produced at the end of the growth season when the cambial activity is slow are narrower, especially in a radial direction, and mostly have thicker walls. The early wood consists of relatively broad cells with large lumina. The differences between these cells and the thick-walled smaller cells, which terminate the growth of the preceding year, emphasizes the growth rings. To the unaided eye these rings are distinguishable because of the differences in colour between the early and late wood. In certain plants, such as *Tilia*, *Ceratonia*, *Spartium junceum*, and *Zygophyllum dumosum* (Fig. 133, no. 5), one to three cell layers between the rings consist of wood-parenchyma cells. The walls of these cells are thinner than those of the neighbouring fibres. In the stems of many plants, such as *Zygophyllum*, for example, this border parenchyma forms a pale line which clearly marks the borders of the growth rings.

ARRANGEMENT OF VESSELS

The arrangement of the vessels in the secondary xylem of dicotyledons is a characteristic feature and is used in the identification of species. When the vessels are more or less equal in diameter and uniformly distributed throughout the wood, or when there is only a gradual change in size and distribution throughout the growth ring, the wood is termed *diffuse-porous wood* (Fig. 133, no. 3; Fig. 134, nos. 1, 3). Examples of species with such wood are *Acer* spp., *Populus alba*, *Acacia cyanophylla*, *Olea europaea*, and *Eucalyptus* spp. When the wood contains vessels of different diameters and in which those produced at the beginning of the season are distinctly larger than those of the late wood, the wood is said to be *ring-porous wood* (Fig. 135, nos. 1, 2). The wood of *Fraxinus* spp.; *Quercus robur*, *Q. ithaburensis*, *Robinia pseudacacia*, and *Pistacia atlantica* may be given as examples of this type of wood. Many intermediate forms occur between the above two extreme types. Environmental conditions and the age of the plant also influence, to a certain extent, the arrangement of the vessels.

FIG. 133. 1–3, Secondary xylem of *Populus deltoides*. 1, Tangential section. ×80. 2, Radial section. ×80. 3, Cross-section. ×65. 4, Radial section of the secondary xylem of *Pinus halepensis* showing tracheids with bordered pits and crassulae. ×400. 5, Cross-section of the secondary xylem of *Zygophyllum dumosum* in which the initial parenchyma on the border between the adjacent growth rings can be distinguished. ×110.


1
2
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Ring-porous wood is thought to be more advanced than diffuse-porous from the phylogenetic point of view. The former is found only in relatively few species and mainly in plants from the northern hemisphere (Gilbert,

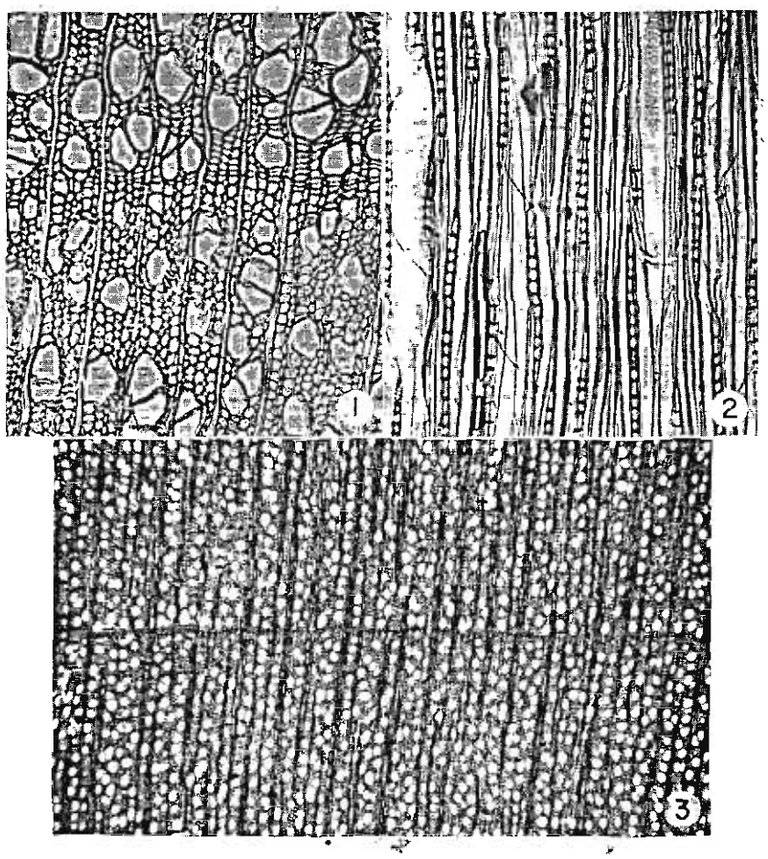

FIG. 134. Diffuse-porous secondary xylem. 1 and 2, Secondary xylem of *Salix babylonica*. 1, Cross-section showing the border between two growth rings. ×100. 2, Tangential section. ×100. 3, Cross-section of the secondary xylem of *Crataegus azarolus* showing the border between two growth rings. ×35.

1940). It has also been recorded that ring-porous wood is relatively common in plants growing in arid habitats (Huber, 1935). This observation is supported by the results of the investigations made on woody plants growing in the Negev. Bailey (1924) suggests that typical ring porosity developed in plants already adapted to tropical environments that became subjected to climates with cold winters or with alternating very dry

and wet seasons. This development is, in other words, connected with seasonal activity.

The pattern of distribution of the vessels is studied in cross-sections

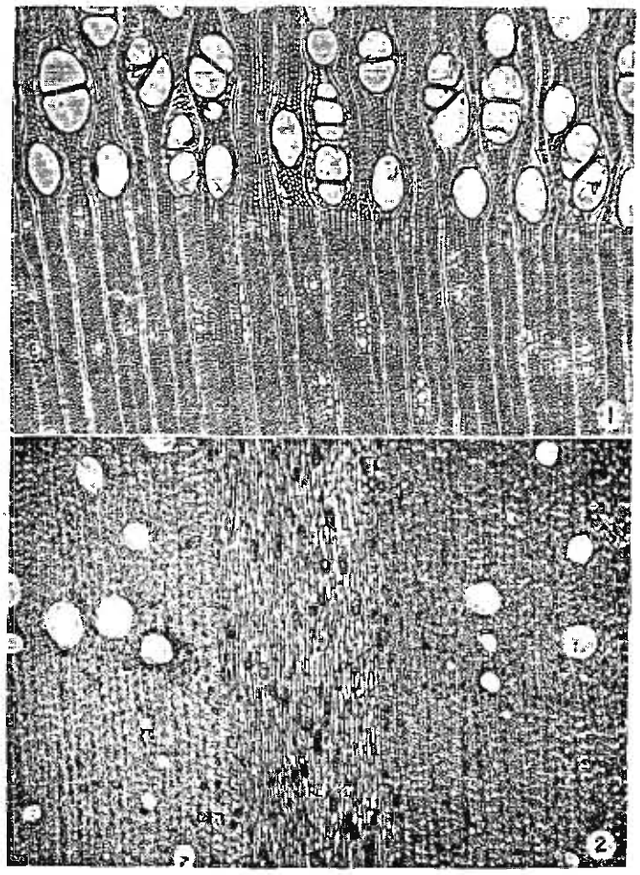

FIG. 135. Ring-porous wood. 1, *Fraxinus syriaca*. ×25. 2, *Quercus ithaburensis*. ×35.

of the wood. Here the vessels can be seen to be single as, for example, in *Eucalyptus* (Fig. 137, no. 1) and *Quercus*, or in groups of different size and shape. For instance, the groups may consist of radial, oblique or tangential rows of two to many vessels, the walls of which are in contact with one another and which are called *multiples* (Fig. 134, no. 1). Such distribution may be seen, for example, in the wood of *Cornus*

and *Populus*. The groups may be in the form of *clusters* (Fig. 138, no. 3; Fig. 140, no. 1), i.e. irregular groups which consist of varying numbers of vessels in both radial and tangential directions. *Pistacia* may be cited as

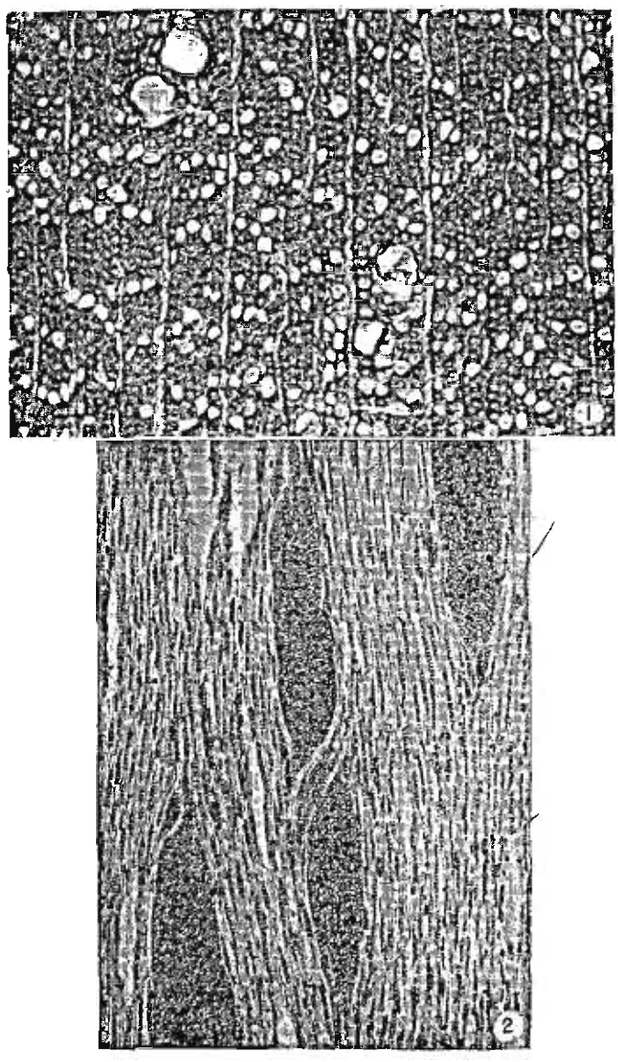

FIG. 136. 1, Cross-section of the secondary xylem of *Quercus boissieri* showin diffuse apotracheal parenchyma. ×120. 2, Tangential section of *Quercus itha burensis* showing small uniseriate and very large multiseriate aggregate rays. ×25

an example of such distribution. The single vessels may be circular or elliptical as seen in cross-section. Vessels arranged in groups are usually flattened where they are in contact with one another.

According to Priestley and Scott (1936), the development of the vessels in early ring-porous wood is very rapid and sudden, while that in diffuse-porous wood is slow. Handley (1936) measured the length of vessels and concluded that the vessels in ring-porous wood are longer than those in diffuse-porous wood. According to Huber (1935), in ring-porous wood

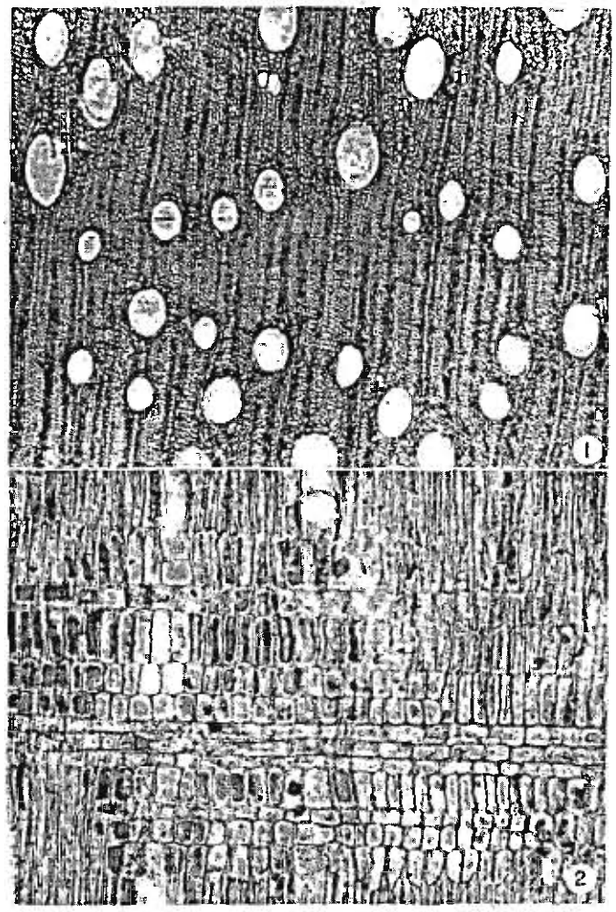

FIG. 137. 1, Cross-section of the secondary xylem of *Eucalyptus camaldulensis* showing the border between two growth rings. ×50. 2, Radial section of the secondary xylem of *Olea europaea* showing a heterogeneous ray. ×150

the transport of water is almost entirely restricted to the outermost ring, and the flow of water in plants with such wood is ten times faster than that in plants with diffuse-porous wood.

It is worth mentioning that, in the light of recent research, it appears that all the vessels of one ring, or even of the entire secondary xylem, are interconnected so that a network is formed (Braun, 1961).

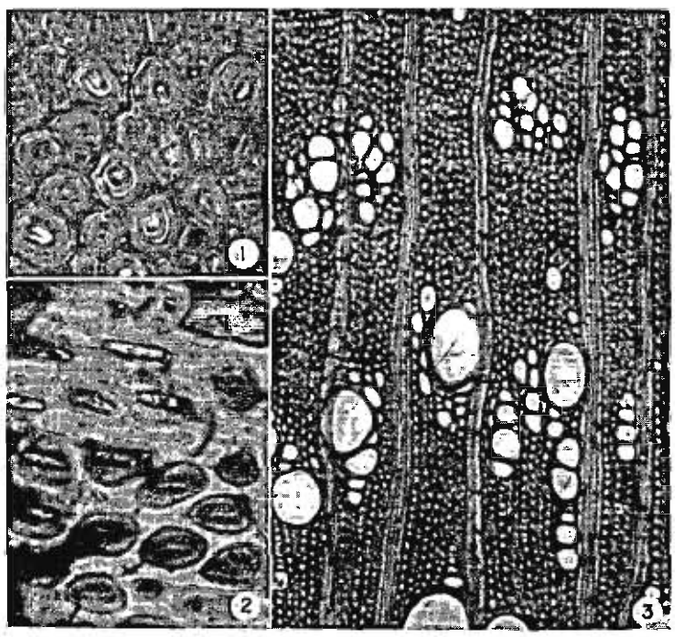

FIG. 138. 1, Cross-section of gelatinous fibres from the secondary xylem of *Acacia raddiana*. ×450. 2, Vestured pits of a vessel of *A. tortilis*, as seen in radial section of the secondary xylem. ×1200. 3, Cross-section of the secondary xylem of *Pistacia atlantica*. ×100.

ARRANGEMENT OF THE AXIAL WOOD PARENCHYMA

The amount of the axial parenchyma varies in the different dicotyledonous species. In some species there is very little axial parenchyma, or it is entirely absent, while in others it constitutes a very large portion of the wood. Apart from the differences in the amount of axial parenchyma there are also differences in its distribution among the other elements of the secondary xylem. Much taxonomic importance is attached to the type of distribution of the axial parenchyma.

There are two basic types of distribution of the axial parenchyma: *apotracheal* (Fig. 136, no. 1) in which the parenchyma is typically inde-

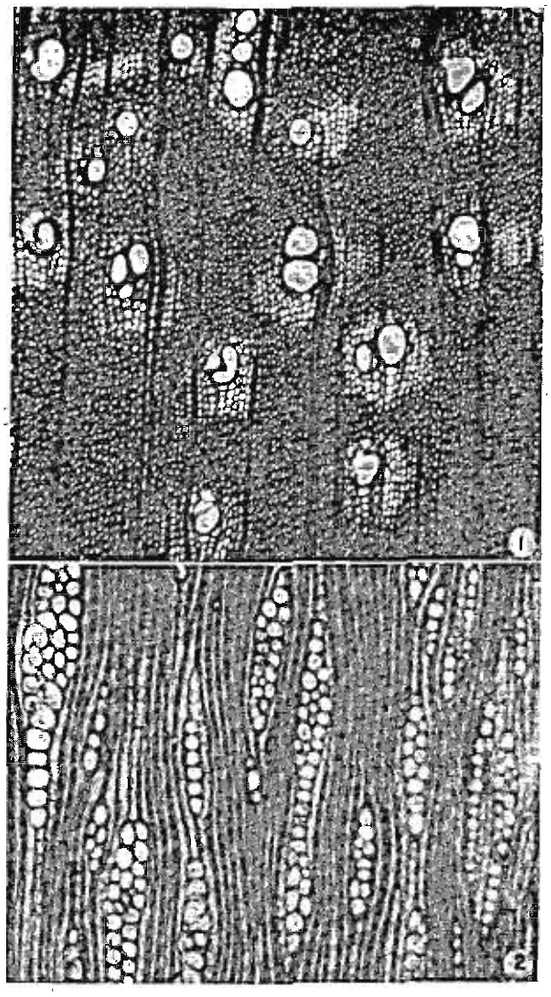

FIG. 139. Secondary xylem of *Acacia cyanophylla*. 1, Cross-section. ×45. 2, Tangential section. ×100.

pendent of the vessels though it may come in contact with them here and there; and *paratracheal* (Fig. 139, no. 1) in which the parenchyma is distinctly associated with the vessels. Both these types are subdivided

into the following variations. When the apotracheal parenchyma is in the form of small uniseriate strands or single cells scattered irregularly among the fibres, it is said to be *diffuse parenchyma* (Fig. 136, no. 1).

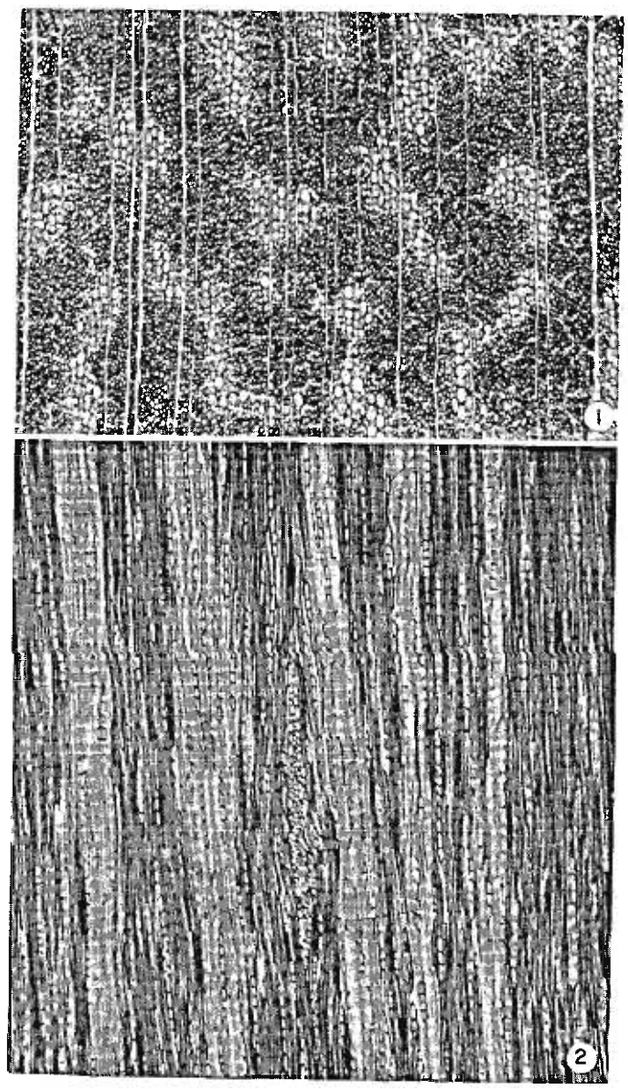

FIG. 140. Secondary xylem of *Thymelaea hirsuta*. 1, Cross-section, showing the small vessels to be arranged in dendritic, diagonal or radial patterns. ×60. 2, Tangential section. ×70.

When, in a cross-section of the wood, the axial parenchyma is seen to form concentric bands, it is said to be *banded* or *metatracheal parenchyma* (Fig. 135, no. 2). Single apotracheal parenchyma cells or those arranged in more or less continuous layers, which may be of variable width, at the end of a growth ring are termed *terminal parenchyma*. Similar parenchyma formed at the beginning of the growth ring is termed *initial parenchyma* (Fig. 133, no. 5). Initial parenchyma occurs in *Ceratonia*, *Zygophyllum* and *Spartium*, for example.

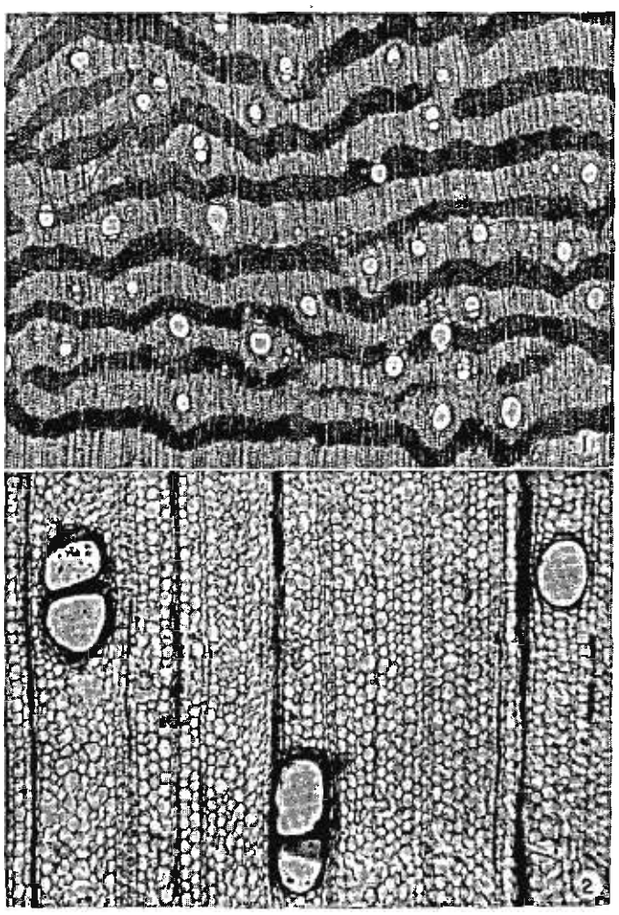

FIG. 141. 1, Cross-section of the secondary xylem of *Acacia albida*, showing broad bands of parenchyma. ×12. 2, Cross-section of the secondary xylem of *Ochroma*. ×40

The paratracheal parenchyma also may be variously distributed. If the parenchyma does not form a continuous sheath around the vessels, as for example in *Acer*, it is said to be *scanty paratracheal parenchyma*. When the paratracheal parenchyma occurs on one side, either external (abaxial) or internal (adaxial), of the vessels it is said to be *unilaterally paratracheal parenchyma*. Parenchyma which forms entire sheaths, of different width, around the vessels, e.g. *Tamarix* (Fig. 129, no. 3), is termed *vasicentric parenchyma*. The shapes of such sheaths as seen in cross-section of the wood may be circular or somewhat elliptical. In some plants, e.g. *Acacia cyanophylla*, *Cercis siliquastrum*, the sheaths in cross-section can be seen to have lateral wing-like extensions (Fig. 139, no. 1); such parenchyma is called *aliform parenchyma*. In the wood of certain species, such as *Acacia raddiana* and *A. albida*, the aliform parenchyma is seen, in cross-section, to form diagonal or tangential bands; this type of parenchyma is termed *confluent parenchyma* (Fig. 141, no. 1).

The distribution of septate wood fibres, if present, is similar to that of the axial parenchyma. In those species that contain a large number of septate fibres there is little axial parenchyma (Spackman and Swamy, 1949).

In certain plants, e.g. *Eucalyptus*, short irregularly shaped tracheids are present in the immediate proximity of the vessels. These tracheids do not, however, form a separate continuous vertical system and they are termed *vasicentric tracheids*.

Kribs (1937) describes the phylogenetic evolution of the axial parenchyma as having taken the following course: (1) from the diffuse apotracheal type, through various intermediate forms and apotracheal banded parenchyma types to paratracheal distribution, and finally, in the most advanced form, to the development of vasicentric parenchyma with numerous cell layers in the sheath; (2) the individual parenchyma cells became shorter and broader with the increased specialization of the secondary xylem, just as in the vessel members. According to Kribs the absence of axial parenchyma is a primitive feature and the presence of terminal parenchyma is an advanced feature which has resulted from reduction.

STRUCTURE OF THE RAYS

In dicotyledons the rays usually consist only of parenchyma cells. On the basis of the orientation of the longest axis of the cells, as seen in radial longitudinal section, parenchyma cells that form the ray may be of one type only or of two types. If the ray cells are all elongated in a radial direction, i.e. if all the cells are procumbent, the ray is *homogeneous*. This type of ray is included, by some workers, with the similar type found in the conifers in the term *homocellular ray*. When the ray in dicotyledonous

wood consists of the two types of cells, i.e. procumbent and square or vertically elongated cells, it is said to be *heterogeneous* (Fig. 130, no. 2; Fig. 137, no. 2). It has been proposed by some workers to include this type of ray with the coniferous rays composed of different cell types in the term *heterocellular ray*.

Heterogeneous rays may be uni- or multiseriate. The most common type of heterogeneous ray is that in which the central portion of the ray is multiseriate and consists of the radially elongated cells, while the upper and lower edges contain the square or vertically elongated cells. Sometimes the radially elongated cells are surrounded by square or vertically elongated cells. There are also a few plants, e.g. *Olea*, in which the square or vertically elongated cells are mingled with the radially elongated cells.

The above nomenclature concerning the structure and arrangement of the elements of the secondary xylem is based on that published by the Committee on Nomenclature of the International Association of Wood Anatomists (Int. Ass. Wood Anatomists, 1947).

It is thought that the presence of two types of rays — uniseriate comprising vertically elongated cells and multiseriate heterogeneous — is a primitive feature from the phylogenetic viewpoint. From this type the many other different types of rays evolved. The evolution was apparently in various directions. One trend has led to the enlargement of the multiseriate rays, while another has been to their reduction in size and number. The uniseriate rays became reduced in height and number. In many plants one type of ray was lost and in a few examples both. In *Quercus* the specialization has resulted in the development of very large multiseriate rays and small uniseriate ones. In *Salix* and *Populus* the phylogenetic specialization is expressed in the development of only one type of ray — the uniseriate. In *Hudsonia* (Cistaceae) and *Aeonium arboreum* (Crassulaceae), for example, the secondary xylem, or at least its inner portion that develops from the cambium in the first years of its activity, is completely devoid of rays. In plants that have such secondary xylem a few uniseriate, noncontinuous rays can be seen in the outer portion of the wood that develops later (Barghoorn, 1941b). From the point of view of cell composition the homogeneous rays are considered to be more advanced than the heterogeneous ones.

The decrease in the size of rays with phylogenetic advancement may have been brought about by changes that took place in the cambium (Barghoorn, 1941a) (Fig. 142, nos. 5–7). Some of the ray initials may become lost and their place be taken up by fusiform initials of the cambium. If this occurs on the ray margins the ray simply becomes narrower, but if it occurs within the ray it results in the splitting of the ray into two or more parts. A ray may also become split as a result of the intrusive growth of the tips of the fusiform initials into a group of ray initials. Further, a ray may become split by the changing of some ray initials into fusiform

initials. In this manner *aggregate rays* (Fig. 136, no. 2) are often formed from large rays. An aggregate ray is defined as a ray comprising a group of small and narrow rays which appears to the unaided eye or under low magnification to be a single large ray.

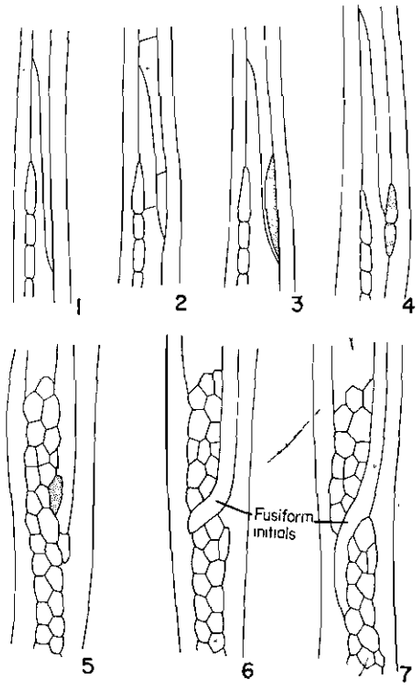

FIG. 142. 1–4, Serial tangential sections of the secondary xylem of *Viburnum odoratissimum* showing the origin of a ray initial at the end of a fusiform initial. Newly formed ray initial stippled. 5–7, Serial tangential sections of the secondary xylem of *Trochodendron aralioides* showing the splitting of a ray by the apical elongation of a fusiform initial. The entry of the fusiform initial into the ray is made possible by the loss of the ray initial that is stippled in no. 5. (Adapted from Barghoorn, 1940.)

As was mentioned above, the rays may also have increased in size during evolution. This enlargement may be brought about by the merging of rays (Fig. 143), by the anticlinal division of the ray initials, or by the horizontal subdivision of the fusiform initials adjacent to the ray so as to form additional ray initials. The merging of rays is brought about by the loss of the fusiform initials that separate the two rays.

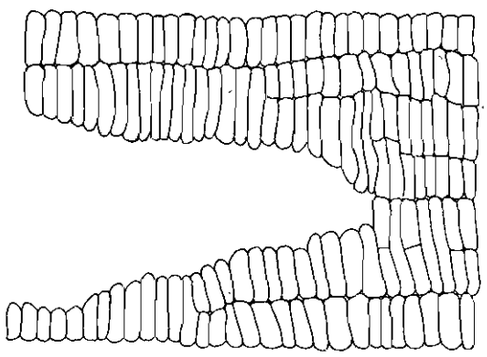

FIG. 143. Radial section of the secondary xylem of *Casearia nitida* illustrating the fusion of two rays by the vertical elongation of the marginal initials and their derivatives. Cambium on right. (Adapted from Barghoorn, 1940.)

GUM DUCTS

Intercellular gum ducts occur in dicotyledonous wood similarly to resin ducts in the gymnosperms (Brown *et al.*, 1949). They may arise normally in the wood or may be the result of various kinds of injury. These ducts contain various substances such as resins, oils, gums and mucilages. Normally-formed gum ducts always occupy a characteristic position in the wood while those of traumatic origin are variously situated. In a given plant the canals may be either horizontal or vertical, but in only a few cases are the two types present in a single plant (cf. Stern, 1954).

Traumatic gum ducts may develop schizogenously, lysigenously or by a combination of both these two methods, i.e. schizo-lysigenously. In the latter case the cavity is first formed by cell division and then it is enlarged by the disintegration of the surrounding cells. The above process of disintegration is termed *gummosis*. Gummosis involves the disintegration of the cell wall carbohydrates and especially of starch, which is present in the cells, to form substances that are collectively known as *gum*. Gums may accumulate in the gum ducts, vessels or other cells of the xylem. Gummosis is often caused by diseases, insect or mechanical injury and physiological disturbances in the plant (Esau, 1953).

Effect of secondary thickening on leaf-traces

As the cambium is situated between the xylem and the phloem, the newly formed xylem continually pushes the phloem and the cambium itself outwards. This results in the separation of the xylem of the inner portion of the leaf-trace, which is situated in the primary body, from its associated

primary phloem. The outer portion of the leaf-trace, therefore, becomes buried in the secondary xylem of the stem (Fig. 144, nos. 1, 2).

With the continued secondary growth and further pushing out of the cortex and the phloem, in which the outer portion of the leaf-trace is situated, the leaf-trace becomes torn into two parts (Fig. 144, no. 3). The tearing of the trace takes place only after the leaf is shed — usually in the first or second season after shedding.

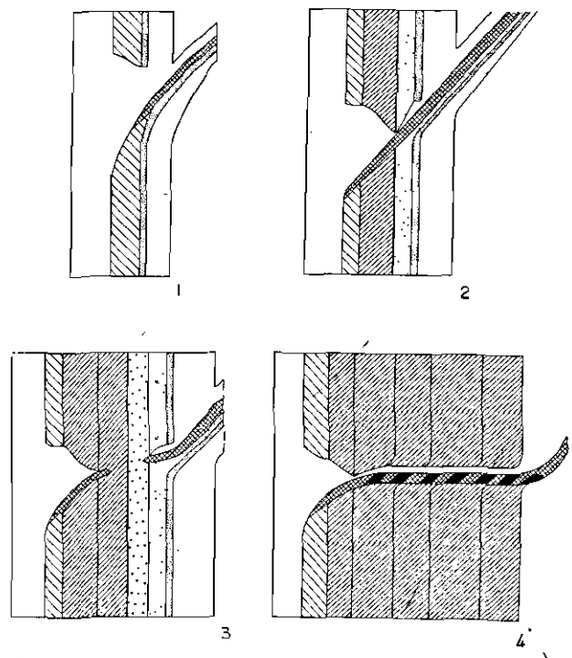

FIG. 144. Diagrams illustrating the relationship of the leaf-trace to the expanding secondary plant body in woody dicotyledons, as seen in radial section. 1, Showing the condition of the leaf-trace in a stem devoid of secondary thickening; the leaf-gap is still open. 2, A stem after 1 year of secondary growth showing that the gap is partly closed by the secondary xylem and phloem. 3, Showing the stem of a deciduous plant after 2 years of secondary growth; the ruptured ends of the trace are separated by secondary vascular tissues. 4, Showing the extension of the leaf trace in an evergreen plant after 5 years secondary growth (parts outside the cambium not represented in this diagram). In this case the trace ruptures from time to time and the gaps thus formed are filled by secondary tissue produced by that part of the cambium on the under side of the trace where it is in contact with the secondary xylem. In the trace the primary tissue is represented by cross-hatching and the secondary tissue by solid black areas. In all the figures primary xylem is represented by widely spaced hatching, secondary xylem by more dense hatching, primary phloem by fine stippling, secondary phloem by coarse stippling, the xylem of the diverging part of the leaf-trace by cross-hatching. (Adapted from Eames and MacDaniels, 1947.)

In evergreen plants the leaf-traces elongate as a result of a special type of secondary growth which is brought about by the addition of new xylem to the middle of the trace. The primary xylem of the leaf base gradually ruptures obliquely (because the leaf-traces pass out, towards the leaves, obliquely through the cortex) and the cambium in that region then adds new cells which replace those destroyed. In *Araucaria*, for example, leaf-traces may reach a considerable length and may pass through several growth rings (Fig. 144, no. 4). In evergreens the trace is ruptured after the leaf is shed as is the case in deciduous plants (Eames and MacDaniels, 1947).

Fibre and tracheid variation within the trunk

The length of fibres and tracheids has been found to increase from the centre of trunk towards its periphery (Gerry, 1915; Stern-Cohen and Fahn, 1964). Fibre length also varies along the trunk: in *Eucalyptus gomphocephala*, for example, the longest fibres were found to occur at a height of about 6 ft above ground level. In a growth ring the late-wood fibres in dicotyledons and tracheids in gymnosperms have been found to be longer than those of the early wood (Kribs, 1928; Bisset *et al.*, 1950; Stern-Cohen and Fahn, 1964). In dicotyledons the variations in fibre length within the same growth ring are probably due to changes which take place during the differentiation of the fibres and are not due to an alteration in size of the fusiform initials in the cambium. Such a view has also been expressed by Chalk *et al.* (1955) as a result of the investigations carried out on trees with storied wood. The increase in wall thickness, and length of the fibres of the late wood is probably the result of the difference in the rate of growth, i.e. the period of differentiation of an element produced toward the end of the growth season is longer than that of one produced at the beginning of the season and, therefore, the elements of the late wood may become longer and have thicker walls (Bisset *et al.*, 1950). The variation in fibre length along the tree as well as from the centre of the trunk toward the cambium in trees with non-storied wood is generally accepted to be connected with the change in size of the fusiform initials.

Comparison of trees growing in mesophytic and arid habitats showed that the dimensions of width, wall thickness and length of the fibres were all larger in the trees growing in the mesophytic habitat (Stern-Cohen and Fahn, 1964).

Growth-ring analysis

The problem of the correlation between the amount of annual increment and the environment arose because of the variations observed in the width of the annual growth rings (Douglass, 1936; Holmsgaard, 1955;

Glock, 1955; Fahn *et al.*, 1963). The many investigations that have been made in this respect suggest that in arid regions the main factor influencing the width of the growth ring is the amount of precipitation, while in the cooler temperate regions, temperature may play an important rôle. It has also been suggested that there is a correlation between the width of the annual rings and the amount of sun-spots. Many authors have tried to draw conclusions as to the history of the climate by growth-ring analysis of very old trees.

Relationship between the microscopic structure and wood properties

The woods of different species possess certain properties which make them suitable for different uses. These properties depend on the histological and chemical structure of the xylem tissue. The histological features that affect the characteristics of the wood are the presence and distribution of vessels, the presence or absence of fibres and their relative number, the diameter of the fibres and thickness of their walls, the length of the fibres and the extent to which they overlap, the form of the fibres — whether straight or curved, the width and number of the rays, and the presence or absence of tyloses.

The chemical structure is of importance in connection with certain properties and especially those by which heartwood differs from sapwood. The cell walls themselves differ in the relative amounts of cellulose, lignin, etc. Tannin compounds may be accumulated in large quantities in the cell walls and the cells may contain different amounts of gum, resins and tannins.

WEIGHT OF WOOD

The specific gravity of the wall substance of the secondary xylem of all plants is more or less the same, and is about 1·53. Therefore the differences in the weight of woods depend on the proportion between the amount of wall substance and lumen. Plants such as *Diospyros*, for example, in which the cell walls are thick and the lumina small and which contain many fibres, have heavy wood. Plants in which the cell walls are thin and in which the lumina of parenchyma and fibres are large, have light wood. In some genera, such as *Populus* and *Tilia*, the specific gravity of the secondary xylem is low although the fibre walls are not particularly thin; in these woods the low specific gravity is due to the presence of numerous thin-walled vessels. An extremely light wood is that of *Ochroma* (balsa wood), which belongs to the type of wood known as "cork-wood". Such wood contains a high proportion of large, thin-walled parenchyma cells (Fig. 141, no. 2).

The specific gravity of wood varies from 0·04 (*Aeschynomene* of the Leguminosae) to about 1·4 (*Krugiodendron* of the Rhamnaceae). The specific gravity of timber commonly used in trade is between 0·35–0·65 (Eames and MacDaniels, 1947). The specific gravity of the wood of some trees growing in Israel is as follows: *Eucalyptus camaldulensis*, 0·52–0·68; *Pinus halepensis*, 0·48; *Ficus sycomorus*, 0·40; *Quercus calliprinos*, 0·80; *Phillyrea media*, 0·79; *Tamarix aphylla*, 0·51.

Of the very light type of wood, balsa wood (*Ochroma*), the specific gravity of which is 0·1–0·16, is much utilized in industry, especially as insulating material in the aircraft and life-boat industries. Balsa wood is strong in relation to its specific gravity. Histologically, two types of light wood can be distinguished: that in which there are bands of lignified, thick-walled cells alternating with bands of non-lignified thin-walled cells, and that in which the above two types of cells are homogeneously arranged (Eames and MacDaniels, 1947). In the wood of certain plants, such as *Carica papaya* and *Phytolacca dioica*, the only lignified elements are the vessels.

STRENGTH

Wood that contains many libriform fibres or fibre-tracheids is a strong wood and therefore it is seen that dense and heavy woods must also be strong woods. The length of the fibres and the degree to which their ends overlap are apparently of less importance to the strength of the wood. According to some workers (Pillow and Luxford, 1937) the orientation of the cellulosic microfibrils in the walls influences the strength of the wood. For example, it is thought that when the microfibrils are so orientated as to be almost parallel to the horizontal axis of the fibre, the wood is weakened.

DURABILITY

The ability of wood to withstand rotting, as a result of bacterial or fungal action, mainly depends on the chemical composition of the wood. The degree of durability is determined by the presence of substances such as resins, tannins and oils in the walls and lumina of the cells. Also, the appearance of tyloses is of some importance, as they block the passage of fungal hyphae as well as of oxygen and water through the vessels.

Wood of trees such as *Sequoia*, *Catalpa*, *Robinia*, *Maclura* and *Castanea* are very durable, while that of trees such as *Populus*, *Acer*, *Tilia* and *Carya* rot very rapidly (Eames and MacDaniels, 1947). The heartwood is usually more resistant to decay than is the sapwood. There is no definite correlation between the depth of colour of wood and its durability, but

generally darker woods are more resistant to decay. The colour is usually an indicator of the amount of preservative substances in the wood.

The ability of wood to remain intact under mechanical strain depends on the hardness and density of the wood.

PLIABILITY

A flexible wood is one in which the wood structure is homogeneous with long straight fibres that overlap for some distance, and with straight rays. Pliability is also influenced by the amount of water in the wood (Pillow and Luxford, 1937).

Many properties of wood are connected with hygroscopic moisture, a factor on which numerous technological problems, the main of which is the dimensional stability of wood, depend. For details of this and other problems of wood technology see Brown, Panshin and Forsaith, Vol. 2, 1952 and Tiemann, 1951.

Grain

Grain is the term used when describing the orientation of the elements in the wood. For instance, if all the elements are orientated parallel to the longitudinal axis of the trunk, the wood is said to be *straight grained*, and if the elements are spirally arranged, *spiral grained*. If there is no perceptible difference between the early and late wood, the wood is *even grained* but when distinct differences exist between the early and late wood, the wood is said to be *uneven grained*.

The designs and patterns that are characteristic of variously sawn woods are termed *figures* (Brown *et al.*, Vol. 1, 1952). These figures are dependent on the grain and its exposure by the direction of sawing.

Wood in which the orientation of the elements is spiral, but in which the spiral is reversed at more or less regular intervals along a single radius, is called *interlocked-grained* wood. A radial cut of such wood results in timber that exhibits a characteristic figure known in commerce as *ribbon* or *stripe figure*. The striped effect of light and dark bands results from the difference in light reflection from the differently orientated elements.

Wavy or *curly figures* are the result of the undulations of the fibres, to the left and right of a radial plane. Such wood when cut tangentially exhibits undulated figures. When the undulations are close to one another and the changes in direction of the fibres are abrupt the pattern obtained is termed *fiddleback figure* as such designs, chiefly from maple and mahogany stock, have long been used in the manufacture of violins.

The figure commonly known as *bird's-eye figure* is produced when wood with numerous conical indentations of the growth rings is cut tangentially.

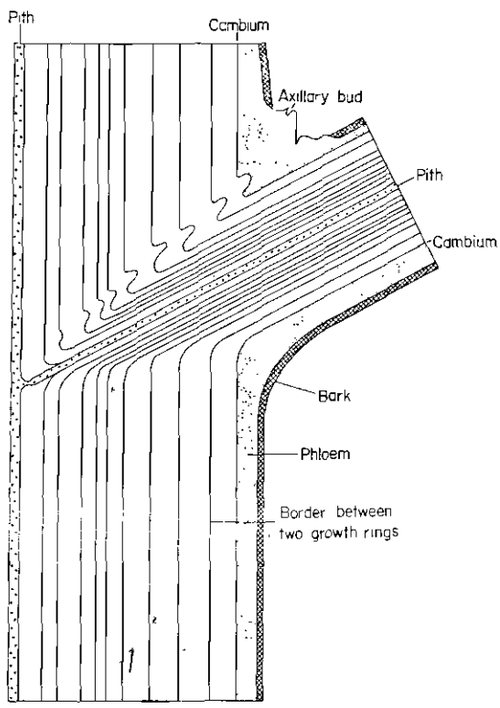

FIG. 145. Diagram illustrating the relationship between the secondary tissues of a branch and main stem. (Adapted from Eames and MacDaniels, 1947.)

Defects in wood resulting from growth stresses

Environmental factors may result in the production of wood with abnormal structure and properties. One type of such abnormal wood is *reaction wood* which develops in leaning trunks and limbs (Wardrop and Dadswell, 1948, Scurfield and Wardrop, 1963; Wardrop and Davies, 1964). This wood brings about the recovery of the organs. There are considerable differences in the place of development, nature and shape of the reaction wood of conifers and that of dicotyledons. In the conifers the reaction wood develops on the underside of the leaning trunk or branch, while in the dicotyledons it develops on the upperside. The reaction wood of the conifers is termed *compression wood*, and that of the dicotyledons *tension wood*. Although these terms emphasize the fact that the reason for the development of the reaction wood is the tension that acts throughout the length of the trunks and branches, it must not be forgotten that other fac-

tors such as light, gravity and the flow of solutions may also influence the formation of such wood. Stresses also exist in erect trees but they are increased in leaning trees.

COMPRESSION WOOD

Compression wood is produced by the local increased activity of the cambium. There is, however, little direct correlation between the amount of compression wood formed and the extent of recovery of the stem. According to some workers a leaning stem can also recover by the production of normal wood in addition to the compression wood. Compression wood is recognizable by the presence of excentric growth rings. Typical compression wood is 15–40% heavier than the normal wood of the same species. In compression as compared with normal wood there is a more gradual transition between early and late wood. The tracheids of compression wood are seen to be rounder in cross-section, and intercellular spaces can be found between them. The microfibrils of cellulose in the secondary wall of these tracheids are orientated in such a way as to form a large angle with the longitudinal axis of the cells. The inner layer of the secondary wall is absent or only slightly developed (Wardrop and Dadswell, 1950), and spiral striations can be seen in the secondary walls. The walls of the compression wood tracheids that are formed in the spring are slightly thicker than those of the normal wood. The compression wood tracheids are usually shorter than those of normal wood. There is usually a somewhat higher lignin content in compression wood than in normal wood. Generally, it is possible to summarize the characteristics of compression wood, in comparison with those of normal wood, as being heavier, more brittle and capable of unusually high and irregular longitudinal shrinkage but of less transverse shrinkage. Because of these differences in shrinkage, lumber containing compression wood twists as it dries out.

TENSION WOOD

Tension wood develops on the upper side of leaning dicotyledonous stems and, similarly to compression wood, the presence of tension wood is recognized in a stem by the formation of eccentric growth rings. This asymmetry is the result of the more rapid or more continuous cambial activity on one side of the stem (Wardrop and Dadswell, 1955). Histologically the distinguishing feature of tension wood is the presence of gelatinous fibres in the early formed wood of the growth rings. The orientation of the cellulosic microfibrils in the outer, non-gelatinous wall layers of the gelatinous fibres is about 45° in relation to the longitudinal axis of the fibres. In the inner, gelatinous layers, the orientation of the microfibrils is almost parallel to the longitudinal axis of the fibre (Münch, 1938;

Wardrop and Dadswell, 1948, 1955). From these facts some workers have concluded that it is the gelatinous wall layers that are mainly responsible for the contraction of the tension wood. There is less lignin in tension wood than in normal wood, but the amount of cellulose and pentosans is higher (see also p. 86).

Two types of tension wood are distinguishable: *compact tension wood* in which the gelatinous fibres are situated in certain regions of the stem (e.g. *Acer*), and *diffuse tension wood* in which single or groups of gelatinous fibres are scattered among the normal fibres (e.g. *Acacia*, Fig. 138, no. 1).

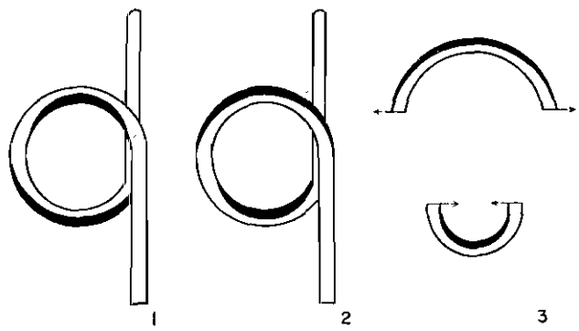

FIG. 146. 1 and 2, Diagrams showing the development of reaction wood (represented by solid black areas) in looped branches. 1, Compression wood. 2, Tension wood. 3, Diagrams illustrating the results obtained when a loop in which tension wood has been formed is cut in half. The arrows indicate the direction of the movement of the cut ends. (Adapted from Jaccard, 1938.)

The strength of the tension wood of the different species varies, but in most cases this wood tends to form horizontal breaks. Some research workers found that such breaks occur in single fibres. When tension wood is sawn the cut surface appears woolly due to the tearing of the groups of gelatinous fibres.

Tension usually exists between the peripheral secondary xylem and that near the centre of the stem. When a piece of stem is cut longitudinally the peripheral parts contract more than those portions nearer the centre. In asymmetric stems containing tension wood the difference in bending is more obvious. In branches that were bent into loops (Fig. 146, nos. 1–3) tension wood was seen to develop on those sides of the loop which were directed upwards. When such a loop was cut, after the formation of the tension wood, contraction again occurred in those places where the tension wood had formed. Similar experiments were made with conifer branches in order to establish the properties of the compression wood (Jaccard, 1938).

The facts gathered from different investigations, and cited by Wardrop (1964), show that not in all cases does the tension wood develop on the upperside of the bent branch or stem. As a result of bending in different ways and directions, it was possible to obtain tension wood on different sides of the same branch. As it became clear from these experiments that a relationship exists between the production of tension wood and the tendency of the stem or branch to shrink longitudinally (Wardrop, 1956), it was possible to understand the fact that tension wood develops in those places where it enables the stem or branches to return to the normal position.

There are several theories that attempt to explain the mechanism by which a bent stem or branch recovers due to the development of the tension wood. According to Frey-Wyssling (1952) it is accomplished by forces in the cambium which far exceed the normal osmotic pressure. According to Münch (1938) the cells shrink because of the characteristic orientation of the cellulose units in the different wall layers. According to Wardrop (1956) the acting force is the volume contraction of the cell wall during the crystallization of the cellulose. None of these theories or any of the others that attempt to explain the mechanism by which bent trunks straighten have been sufficiently proved as yet.

An example of a key by which trees and shrubs may be identified according to the structure of the secondary xylem

As has already been discussed, the secondary xylem of the different species varies in the shape, size, arrangement and relative amounts of its constituent elements. Usually there is a connection between the similarity of the internal structure of the wood and the genetic relationship of the plants (cf. Metcalfe and Chalk, 1950). This variability and similarity make it possible to devise a key by which the plant species can be identified according to the structure of their secondary xylem only. This possibility of identifying the botanical species from a piece of timber is of great taxonomic as well as commercial and industrial importance. This method has also been used to identify the wood from which objects found in archeological excavations were made.

There are different ways in which such a key may be made, including the use of a punched-card system (Clarke, 1938a, b; Phillips, 1948). Following is an example of a dichotomous key in which a small number of the trees and shrubs growing in Israel can be determined. In such a key two alternatives are given at each stage. Only one of the alternatives will be entirely applicable to the wood in question. This alternative leads to another stage in the key from which the wood may be identified immediately, or which

leads to further alternatives from which the wood can eventually be identified.

1. Wood lacking vessels (gymnosperms) 2
–. Wood with vessels (dicotyledons) 4
2. Resin ducts present in each growth ring..... *Pinus*
–. Resin ducts not present in all growth rings (only present in case of injury), or completely absent 3
3. Resin ducts sometimes present; tori with lobed edges..... *Cedrus*
–. Resin ducts never present; tori not as above.....*Cupressus*
4. (1) Included phloem present 5
–. Included phloem absent 6
5. Rays contain cells that are radially elongated..... *Salvadora*
–. Rays lacking; sometimes the wood parenchyma may be arranged in short radial rows similar to rays ..... *Bougainvillea* and genera of the Chenopodiaceae
6. (4) Growth rings not distinct 7
–. Growth rings distinct 8
7. Rays clearly heterogeneous .....*Ficus sycomorus*
–. Rays almost homogeneous .....*Acacia raddiana* *A. tortilis*
8. (6) Wood more or less distinctly ring-porous — the vessels formed at the beginning of the season are conspicuously larger than those formed later and this may be seen without the aid of a microscope 9
–. Wood diffuse-porous — the diameter of the vessels almost equal throughout the growth ring, or gradually smaller toward the termination of the ring 13
9. Vessels single or arranged in multiples of 2–4. Rays 2–3 cells wide. Paratracheal wood parenchyma around the narrow vessels is aliform-confluent ..... *Fraxinus*
–. Vessels and wood parenchyma not arranged as above..... 10
10. Wood rays 1–4 cells wide 11
–. Large wood rays wider than 4 cells 12
11. Vasicentric parenchyma scanty ..... *Pistacia*
–. Vasicentric parenchyma aliform to aliform-confluent..... *Cercis*
12. (10) Large, aggregate, multiseriate rays (more than 20 cells wide) present; vessels devoid of gum deposits ..... *Quercus*
–. Rays not aggregate, less than 10 cells wide; vessels filled with gums ..... *Prunus amygdalus*
13. (8) Rays not wider than one cell 14
–. Rays wider than one cell 15
14. Rays homogeneous ..... *Populus*
–. Rays heterogeneous ..... *Salix*
15. (13) Maximum width of the rays exceeds 6 cells 16
–. Maximum width of rays less than 4 cells 18

16. Wood parenchyma storied, paratracheal and vasicentric ... *Tamarix*
–. Wood parenchyma not as above 17
17. Height of large rays exceeds 70 cells; in cross-section of wood the rays widen perceptibly between growth rings. Vessels are not filled with gum ..... *Platanus*
–. Height of large rays less than 60 cells; rays do not widen perceptibly. Most vessels filled with gum ..... *Prunus amygdalus*
18. (15) Apotracheal terminal and paratracheal vasicentric wood parenchyma present. Vessels mostly arranged in multiples of 2–6 vessels 19
–. Wood not as above 20
19. Spiral thickening clearly visible on inner pitted walls of the vessels. Diameter of the early-formed vessels greater than that of the later-formed vessels ..... *Cercis*
–. Spiral thickening not present on inner walls of vessels. Early and late-formed vessels of same diameter ..... *Ceratonia*
20. (18) Rays conspicuously heterogeneous; several rows of radially elongated cells alternate with several rows of vertically elongated cells ..... *Olea*
–. Rays not as above 21
21. Vessels single ..... *Eucalyptus*
–. Most of the vessels arranged in multiples ..... *Acer*

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CHAPTER 16

SECONDARY PHLOEM

THE arrangement of the elements of the secondary phloem is parallel to that of the secondary xylem. In the phloem there are also two systems, the vertical and horizontal, which are derived from those initials that give rise to the similar systems in the xylem.

The principal components of the vertical system of the phloem are the sieve elements, phloem parenchyma and phloem fibres. The horizontal system comprises the parenchyma of the phloem rays.

Storied, non-storied and intermediate arrangements of the elements can also be distinguished in the phloem. As in the xylem, the arrangement of the tissue is primarily determined by the nature of the cambium, i.e. whether it is storied or not. Secondly, the arrangement is determined by the extent of elongation of the various elements of the vertical system during the differentiation of the cells.

In many species of dicotyledonous trees growth rings may also be observed in the phloem, but they are less distinct than those seen in the xylem. The growth rings, as seen in the phloem, are due to the differences in the cells produced at the beginning and at the end of the season — at the beginning of the growth season the cells are conspicuously extended radially, while those produced at the end of the season are flattened. The arrangement of growth rings becomes obscured after some growth seasons as a result of the obliteration of the sieve elements, which cease to function, and because of the changes that take place in the other cells. These changes involve the enlargement of the parenchyma cells, for instance. In many gymnosperms and angiosperms, tangential bands of fibres are developed in the secondary phloem (Fig. 147, no. 2). The number of these bands is not constant in each season and therefore they cannot be used as an indication of the age of the secondary phloem (Esau, 1948; Huber, 1949; Artschwager, 1950).

The ray initials in the cambium produce cells both towards the xylem and the phloem (Fig. 121, no. 2), so that the xylem and phloem rays are continuous. In the vicinity of the cambium the xylem and phloem rays are equal in size, but in many plants the mature outer portions of the phloem rays are of increased width (Fig. 147, no. 1). This feature is, of course, connected with the increase in circumference of the trunk as a result of secondary thickening. The widening of the phloem rays may be accom-

plished solely by the lateral expansion of the existing cells or, as is more common, by the increase, as a result of radial cell division, of the number of cells on the periphery. These widened parts of the rays constitute the expansion tissue which is discussed more fully in the following chapter.

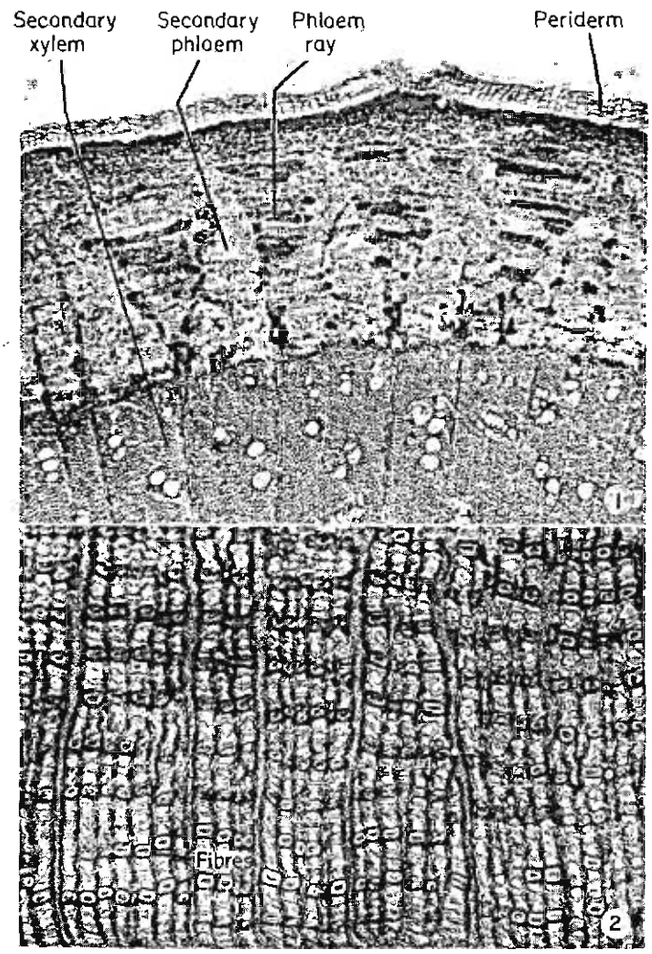

FIG. 147. 1, Micrograph of the outer portion of the stem of *Gossypium* in which the widening of the vascular ray towards the periderm can be distinguished. ×27. 2, Cross-section of the secondary phloem of *Cupressus sempervirens* in which bands of phloem fibres can be seen to alternate with bands of phloem parenchyma and sieve cells. ×120.

Sometimes only some rays become enlarged, while others do not change. The outer parts of the phloem rays become cut off from the inner portions by the development of cork tissue. This tissue is produced by the phellogen, and its formation results in the interruption of the connection between the inner living layers of the phloem and the outer layers which dry out.

Secondary phloem of conifers

As in the secondary xylem, the secondary phloem of the conifers is of relatively simple structure. The vertical system is comprised of sieve cells and parenchyma cells, including albuminous cells (see Chapter 8), and in many plants fibres are also present. The phloem rays of the conifers are usually uniseriate and they usually consist of parenchyma cells only, but sometimes albuminous cells may also be present. The radial arrangement of the secondary phloem elements of the conifers is retained, even in the mature regions, because the elements do not change their shape much during differentiation. The ends of the sieve cells overlap one another and lengthwise each sieve cell comes into contact with a few rays. As in the distribution of the pits on the tracheids, there are more sieve areas on the overlapping end portions of the sieve cells than there are on the other portions of these cells. Usually the sieve areas develop on the radial walls of the sieve cells. The parenchyma cells, with the exception of the albuminous cells (Srivastava, 1963), of the vertical system store starch at certain seasons of the year and many of them contain resins, tannins and also crystals. In the Pinaceae the cells of the phloem parenchyma develop in tangential rows or bands. In the Cupressaceae and Taxodiaceae there are alternating bands of phloem parenchyma, sieve cells and fibres (Fig. 147, no. 2). The secondary phloem of the Pinaceae contains no fibres but the sieve cells are thick walled (Abbe and Crafts, 1939). Resin ducts may be present in the secondary phloem of the conifers. In some conifers, e.g. *Abies balsamea*, these schizogenous ducts form blisters in the secondary phloem which can be seen externally on the bark of the trunk. This resin, known as Canada balsam, is used as a mounting medium in microscopy because its refractive index is the same as that of glass.

For further details on the structure and development of the secondary phloem of conifers refer to Srivastava (1963).

Secondary phloem of dicotyledons

As in the secondary xylem of the dicotyledons, the secondary phloem has a relatively complicated structure. The vertical system contains sieve-tube members, companion cells, parenchyma cells and fibres. The horizontal system consists of variously sized rays, from uni- to multiseriate.

which consist of parenchyma cells only. In both systems, sclereids, lysigenous or schizogenous secretory structures, laticifers and other cells that contain special substances may be present. Many of the parenchyma cells contain crystals and sometimes such cells become subdivided to form chambers, each of which contains a single crystal. Crystals may also be formed in the rays and in the sclerenchyma cells of the phloem.

The secondary phloem fibres of dicotyledons are variously arranged. In *Carya*, which has a hard bark, the fibres constitute the largest portion of the phloem and they enclose among them scattered groups of the other phloem elements. In *Vitis*, for example, the fibres, a great proportion of which are septate, are arranged in tangential bands which alternate with bands of the sieve tubes, companion cells and phloem parenchyma. In *Laurus*, *Nicotiana* and *Stenolobium* there are few fibres and they are scattered among the rest of the elements of the vertical system. In *Aristolochia* no fibres are present.

Phloem fibres that do not develop directly from fusiform cambial initials but from parenchyma cells of non-functioning phloem have been termed *fibre-sclereids* (Esau *et al.*, 1953). Fibre-sclereids occur, for example, in the secondary phloem of *Pyrus malus* (Evert, 1963).

Sclereids occur both in functioning and non-functioning phloem where they arise from parenchyma cells. In secondary phloem the sclereids may occur separately from, or together with, the fibres. In *Platanus* and *Fagus*, for example, the sclereids are the only sclerified elements present in the secondary phloem. In functioning phloem, sclereids are usually not as abundant as are the fibres, but in many species the parenchyma cells of the non-functioning phloem differentiate into sclereids. In certain plants, such as *Prunus*, for example, there is no sclerenchyma in the functioning phloem, but, in the phloem which has ceased to conduct, both fibres and sclereids differentiate.

The arrangement of the sieve tubes and the parenchyma cells differs in various plants. The sieve tubes and parenchyma cells may form separate alternating bands as in *Robinia* and *Aristolochia*, for example, or sieve tubes may be arranged in radial rows as in *Prunus*.

In the sieve-tube members, the sieve areas are distinctly better developed on the sieve plates than on the lateral walls. However, in some plants, e.g. the subfamily Pomoideae of the Rosaceae, this difference is relatively slight. In genera such as *Quercus*, *Juglans*, *Vitis* and *Populus*, the secondary phloem is not storied and the sieve-tube members are elongated and bear mostly compound sieve plates on the oblique end walls. In *Acer*, for example, the sieve-tube members are shorter than the above and the end walls are only slightly oblique and they bear simple sieve plates. In *Robinia*, *Tamarix*, *Ulmus* and *Fraxinus* the simple sieve plates are horizontal. In *Robinia* and *Tamarix* the phloem is storied and the sieve-tube members are short. The oblique end walls are usually so orientated that, in a

radial longitudinal section of the stem, the surface of the sieve plate is seen, and in a tangential section, the sieve plates are sectioned longitudinally. This arrangement is well demonstrated in *Vitis*, for example.

Duration of the activity of secondary phloem

In most dicotyledons the functioning part of the phloem is restricted to that secondary phloem that is produced in the last growth season. Sometimes before the cambium begins to produce new phloem all or most of the sieve elements produced in the previous season cease to function. However, in some plants, e.g. *Tilia*, the sieve tubes are active throughout a number of years and no changes have been observed to take place during the winter. In *Vitis* the phloem was observed to be active for two seasons, but, unlike *Tilia*, *Vitis* lays down thick layers of callose with the onset of winter. These layers are subsequently resorbed in the spring before the renewal of cambial activity (Esau, 1948; Bernstein and Fahn, 1960). It should be mentioned that in plants with included phloem, e.g. *Bougainvillea* and the woody species of the Chenopodiaceae, the phloem strands remain active for many years. The duration of the activity of the phloem in the secondary bundles of the long-lived monocotyledons has yet to be investigated. In most conifers the activity of the phloem elements is also restricted to a single growing season (Esau, 1953).

That part of the secondary phloem in which the sieve tubes no longer serve as a conducting system has been termed *non-functioning* or *inactive phloem* (Esau, 1950). In many plants the parenchyma cells in this phloem remain viable and continue to store starch until such time when the region is cut off from the more central region by the formation of the periderm. The characteristic features of the non-functioning phloem are the presence of thick layers of callose termed *definitive callus*, which cover the sieve areas, the disorganization and disintegration of the protoplast, and the collapse and crushing of the elements, especially in the older regions of the phloem. The definitive callus may not always be seen as it tends to peel away. The most definite indication of non-functioning phloem is the presence of crushed elements. The companion cells cease to function together with the sieve tubes to which they are attached.

In certain plants, e.g. *Robinia pseudacacia* and some species of *Pinus*, the non-functioning phloem contains only a narrow band of intact phloem elements. In *Populus* and *Tilia* crushed sieve tubes are found only a great distance from the cambium and, although only the sieve tubes close to the cambium function, the shape of the non-functioning sieve tubes is retained. In *Salix* the sieve tubes are never obliterated and their shape and size is retained even after the formation of the periderm which separates them from the inner tissues.

In *Vitis vinifera* the non-functioning sieve tubes become filled with tylose-like proliferations from the neighbouring parenchyma cells (Esau, 1948).

The amount of non-functioning phloem that accumulates depends on the manner in which the phellogen is formed. If the phellogen is formed close to the stem surface and when it is not replaced for many years by deeper-formed phellogens, the stem may be encircled by a thick layer of non-functioning phloem (e.g. *Prunus*). If new, more deeply formed phellogens are formed annually within the phloem, e.g. *Vitis*, there is no accumulation of non-functioning secondary phloem.

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CHAPTER 17

PERIDERM

THE development of the secondary vascular tissue is usually accompanied by the formation of cork. Functionally this cork tissue forms a protective layer which replaces the epidermis which dies and is shed. Cork usually forms in the roots and stems of dicotyledons that have continuous and pronounced secondary thickening, but it is usually not formed on leaves, with the exception of the scales of winter buds of certain plants. In the rhizomes of some pteridophytes, e.g. *Ophioglossum*, the epidermis and underlying outer cortical cells become suberized.

Cork is part of the compound secondary tissue which is termed the *periderm* (Fig. 147, no. 1; Fig. 148, no. 1). The periderm usually consists of three parts: the *phellogen* which is the cork cambium; the *phellem* which is the cork and which is produced centrifugally by the phellogen; and the *phelloderm* which is the parenchymatous tissue produced centripetally by the phellogen.

The development of the periderm sometimes commences only after the production of the secondary vascular tissues has reached considerable dimensions. In such cases the circumference of the epidermis increases together with the secondary and other tissues on the outer side of the cambium. Examples of trees with the above type of development are *Laurus*, *Citrus*, *Cornus*, some species of *Eucalyptus*, *Acer* and *Acacia*. In *Viscum*, for example, cork tissue is never formed and the epidermis, the cell walls of which thicken, increases in circumference and persists on the stem throughout the life of the plant.

In addition to the above-mentioned places cork tissue also develops at the place of leaf abscission, around those areas of the plant which are damaged by disease and below wounds.

Structure of the periderm components

PHELLOGEN

The phellogen is a secondary meristematic tissue from all points of view—it originates from cells that have undergone differentiation and it produces tissues that comprise part of the secondary plant body. According

to its position, the phellogen is a lateral meristem as, like the cambium, it results in an increase of the diameter of the axis by periclinal divisions in its cells. Histologically the phellogen is simpler than the vascular cambium as it consists of only one type of initial. These cells appear rectangular in cross-section with their shorter axis in the radial direction and, in longitudinal tangential section, they are seen to be regular polygons. The protoplasts of the phellogen cells contain variously sized vacuoles and they may contain chloroplasts and tannins. There are no intercellular spaces in the phellogen except in those regions where lenticels develop.

PHELLEM

Like the cells of the phellogen, the cells of the phellem (the cork cells) are usually polygonal as seen in tangential section and, in cross-section, they are flattened radially. In cross-section (Fig. 148, nos. 1, 2), the cork cells are usually seen to be arranged in compact radial rows which are devoid of intercellular spaces. This radial arrangement indicates that the phellogen cells divide tangentially.

Cork cells are dead cells. Various types of cork cells can be distinguished and in a few plants crystal-containing cells and sclereids may be found among the cork cells. Sometimes non-suberized cells, which are termed *phelloids*, occur in the phellem. Two common types of cork cells are those which are hollow, thin-walled and somewhat widened radially, and those which are thick-walled and radially flattened. The cells of the latter type may often be filled with dark resiniferous or tanniniferous substances as, for example, can be seen in *Eucalyptus*. These two types of phellem cells may occur together in the same plant as, for example, in *Arbutus* and *Betula* where they occur in alternating layers. In *Betula* this feature causes the cork to peel like sheets of paper.

The primary wall of the phellem cells consists of cellulose and may sometimes also contain lignin or suberin. Internally the primary wall is lined by a relatively thick layer of suberin, which is termed the *suberin lamella*. A thin cellulose layer, which in certain plants may be lignified, may be present on the inside of this lamella. In the thin-walled phellem cells this inner layer of cellulose is absent (Eames and MacDaniels, 1947). The suberin lamella is impermeable to water and gases, and it withstands the action of acids. The protoplast of the phellem cells is lost after the various wall layers have been formed and the cell lumen becomes filled with air or the pigmented substances mentioned above.

In the phellem of some plants, e.g. species of *Haloxylon* and *Anabasis* (Fig. 148, no. 7), bands or large groups of hollow, thick-walled cells occur among the usual thin-walled cork cells. These cells have a lignified primary wall and a thick outer layer of secondary wall on the inside of

which is a relatively thin suberin lamella. This suberin lamella, in turn, is lined by a thinnish cellulose layer which may sometimes be lignified.

The cork tissue of certain plants, such as that of *Quercus suber*, for example, is very elastic, but the cork of most plants lacks this quality.

PHELLODERM

The phelloderm cells are living cells with non-suberized walls. They are similar to the parenchyma cells of the cortex but, if the phelloderm is multiseriate, they are usually arranged in radial rows. In certain plants the phelloderm cells contain chloroplasts and they are photosynthetic. These cells may also store starch. Sclereids and other special cells are sometimes present among the phelloderm cells.

Development of periderm

The phellogen may develop in living epidermal (Fig. 148, no. 2), parenchyma or collenchyma cells (Fig. 148, no. 1). The cells become meristematic and undergo periclinal division. With the commencement of these divisions starch and tannins are gradually lost from those cells that contained them. As a result of the first periclinal division two cells, which are similar in appearance, are formed. The inner cell is capable of further division, but often it does not do so. In both cases, however, this cell is regarded as a phelloderm cell. The outer cell undergoes a periclinal division resulting in the formation of two cells. The outer of these two cells differentiates into a cork cell and the inner cell constitutes the phellogen initial and continues to divide. Sometimes the cork and phellogen cells are formed after the first division and then no phelloderm cell is formed. In addition to periclinal divisions the initials of the phellogen undergo occasional anticlinal divisions, so that the circumference of the cork cylinder is continuously increased.

The number of phellem layers is usually greater than the number of phelloderm layers. In certain plants the phelloderm is completely absent but in many plants it consists of one to three layers of cells, while in a few other plants it may be up to six layers thick. The number of layers in the phelloderm may also alter with the age of the plant. The number of layers of phellem cells produced in a single season varies, in different species, and may be very large. If the first-formed periderm remains on the axial organ for many years, the outer layers of cork become cracked and are shed so that the layer of cork remaining on a plant is of more or less constant thickness.

In certain plants, such as *Quercus suber* and *Aristolochia*, thick layers

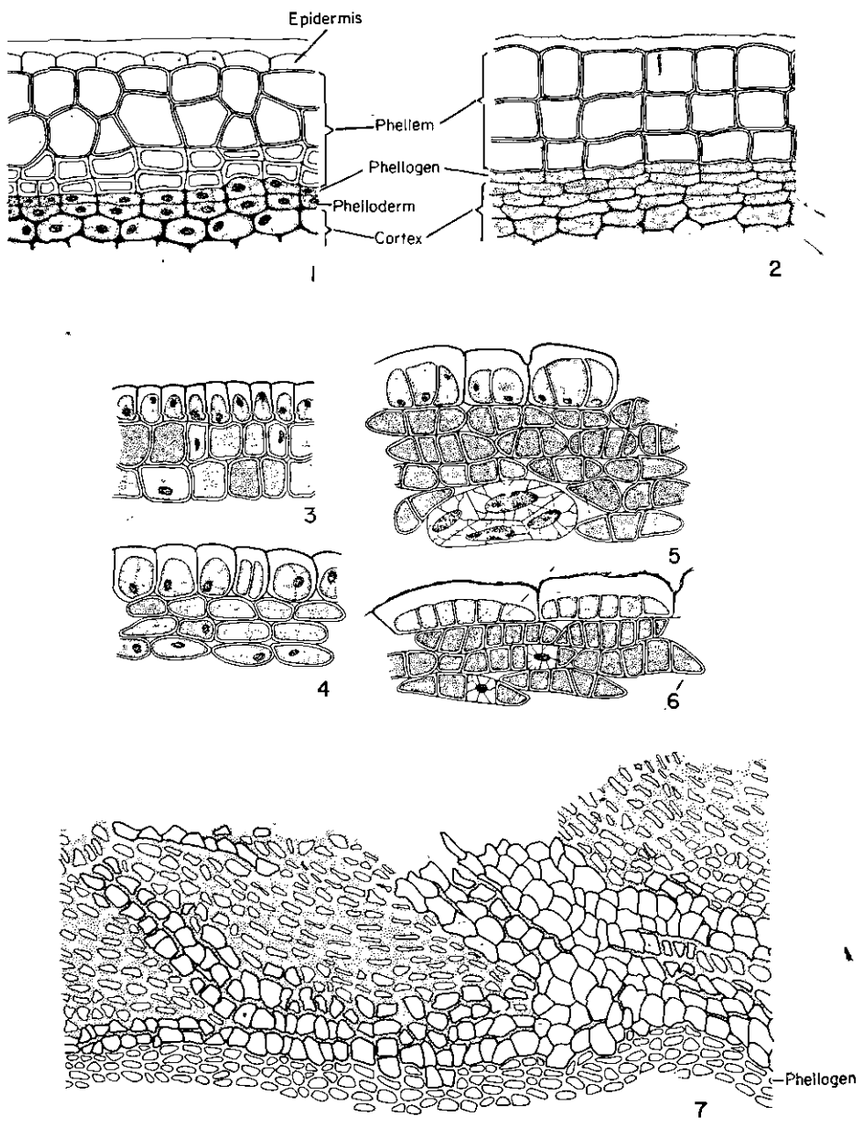

FIG. 148. 1, Outermost portion of a cross-section of a branch of *Populus deltoides* showing the development of the phellogen in the outermost layer of the cortex. 2, As above but of *Solanum dulcamara* in which the phellogen develops in the epidermis. The phellogen is formed from the inner cells resulting from a periclinal division of the epidermal cells; the outer cells form the outermost layer of the phellem and are covered by cuticle. No phelloderm is formed. 3–6, Portions of

of cork are added on the surface of the stems. The first-formed periderms, which are replaced by more-internal periderms, are relatively thin and contain only a few layers of cork cells.

In most dicotyledons and gymnosperms the first periderm is usually developed in the first year of growth of the axial organ on those portions which have ceased to elongate. Periderm formed on young organs develops at the same time all over the circumference to form an entire cylinder, while periderms that are formed on older organs usually start to develop in isolated patches from which the activity spreads laterally, and it may take some years till the cork tissue forms an entire cylinder.

Location of phellogen formation

As has already been mentioned above, the periderm replaces the primary protective tissues (epidermis and cortex) of the axial organs. With the continuation of the process of secondary thickening the periderms themselves are replaced, from time to time, by new periderms which are formed each time deeper in the living tissues of the axis. Therefore, it is necessary to distinguish between the first periderm and those that are formed later.

The development of the first phellogen may take place in different cell layers external to the vascular cambium. In many stems, e.g. *Solanum dulcamara*, *Quercus suber* and *Nerium oleander*, the first phellogen is formed in the epidermis itself (Fig. 148, no. 2). More commonly the first phellogen develops in the layer of cells immediately below the epidermis. Such development can be seen in *Populus* (Fig. 148, no. 1), *Juglans* and *Ulmus*, among others. In the potato tuber, the phellogen develops in the epidermis as well as in the subepidermal cell layer, but the phellogen formed in the epidermis does not continue to function after its formation. In the stems of certain plants, e.g. *Robinia pseudacacia*, species of *Aristolochia* and *Pinus*, the first phellogen forms in the second or third cortical layers. In *Thuja*, *Punica*, *Arbutus*, *Vitis* and *Anabasis* the cambium of the first-formed periderm develops near the phloem or in the phloem parenchyma itself. In roots of gymnosperms and dicotyledons, the first phellogen is characteristically formed in inner layers, usually in the pericycle. In the roots of

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the outermost layers as seen in cross-section of the stem of *Eucalyptus gigantea* showing various stages in the anticlinal division of the epidermal and cortical cells; the divisions bring about the increase in the circumference of the organ. In the early stages groups of cells related to a single mother cell can be distinguished. 7, Portion of a cross-section of the periderm of *Anabasis articulata*, in which two types of phellem cells—thin walled and thick walled—can be seen. Thickened walls stippled. (Nos. 1 and 2, adapted from Eames and MacDaniels, 1947; nos. 3–6, adapted from Chattaway, 1953.)

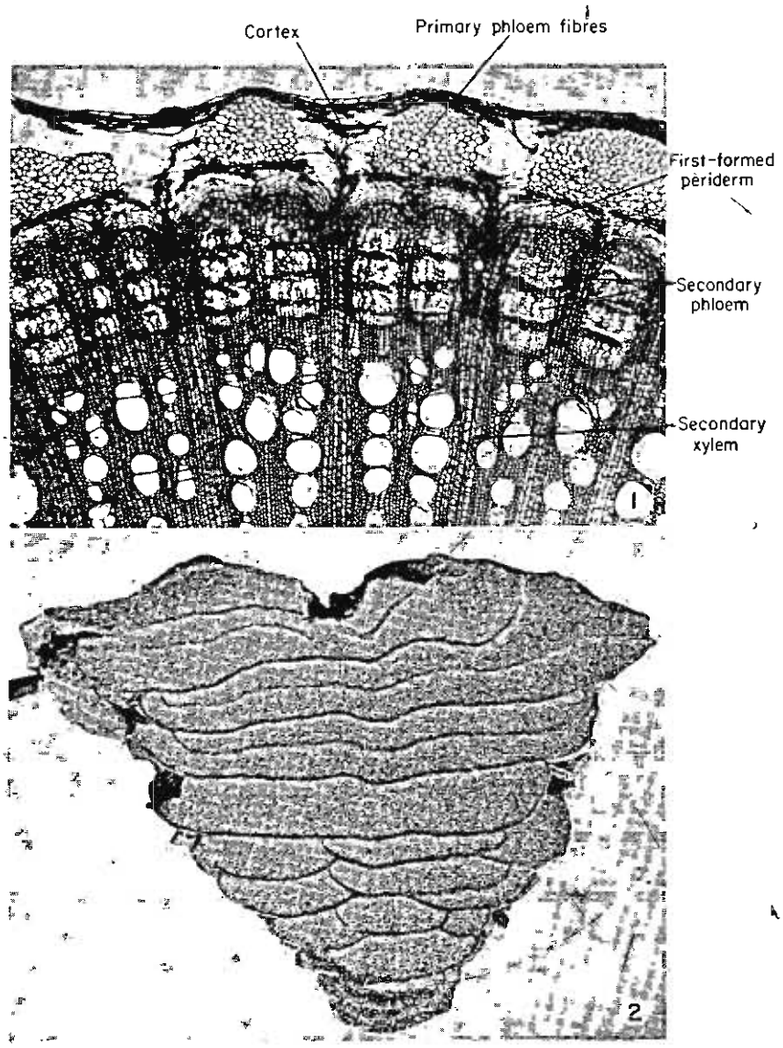

FIG. 149. 1, Micrograph of the outer portion of a cross-section of a branch of *Vitis vinifera* showing the first-formed periderm to develop in the phloem parenchyma. ×35. 2, Photograph of a cross-section of rhytidome of *Pinus* showing scale-shaped additional periderms. The periderms are distinguishable as dark lines ×6.

monocotyledons the first phellogen usually develops in the outer layers of the cortex.

If subsequent periderms form one within the other, one additional phellogen may be produced in each growth season. The later-formed periderms each develop deeper in the cortex or primary phloem and, with continued secondary thickening, deeper and deeper within the secondary phloem. Two types of formation of subsequent periderms may be distinguished. In those plants in which the first-formed periderm develops in an inner layer, e.g. *Vitis*, the additional periderms usually form entire cylinders similar to the first-formed periderm, while in plants in which the first periderm is formed in the epidermis or the outer layers of the cortex, e.g. *Pinus*, the additional periderms develop in the form of scales or shells, the concave side of which is directed outwards (Fig. 149, no. 2; Fig. 150, nos. 1–5).

In certain genera the subsequent periderm already begins to develop in the first year of growth of the stem or branch. In apple and pear trees subsequent periderms begin to develop in the sixth or eighth year of growth and, according to Evert (1963), the first phellogen may even remain active for about 20 years. In *Punica* and in a few species of *Populus* and *Prunus* the first-formed phellogen may remain active for 20 or 30 years, while on *Quercus suber*, some species of *Fagus*, *Anabasis* and *Haloxylon*, and in a few other genera and species, normally no subsequent phellogens are formed during the life of the plant. In *Quercus suber* and other species in which the first phellogen is active throughout the entire life of the plant, or for many years, there are seasonal differences in the types of phellem cells produced. As a result of this, bands, which can apparently be regarded as annual growth rings of phellem, are developed. In bottle corks such annual rings can be well demonstrated (Fig. 152, no. 1).

In roots the first-formed periderm may persist as a continuous layer over the entire length of the organ, with the exception of the tips. The increase in diameter of the cork cylinder is brought about by anticlinal divisions in the phellogen cells and in the living cells below them. Usually the cork of roots is thin and smooth. The conditions in the soil apparently hasten the rotting and sloughing of the cracked outer portions of the cork. In the roots of many herbaceous plants no periderm is formed, but the outer layers of cells become suberized (i.e. deposits of suberin are laid down in the cell walls).

In certain plants, as, for example, many species of *Artemisia* and especially those from arid regions (Moss, 1940; Moss and Gorham, 1953) and in *Achillea fragrantissima*, layers of cork cells occur in the secondary xylem, on the borders of the annual growth rings.

With the formation of each subsequent periderm the tissues exterior to it become cut off from the nutrient and water supply and so die. As a result of this a hard, outer crust develops on the periphery of the axis. This

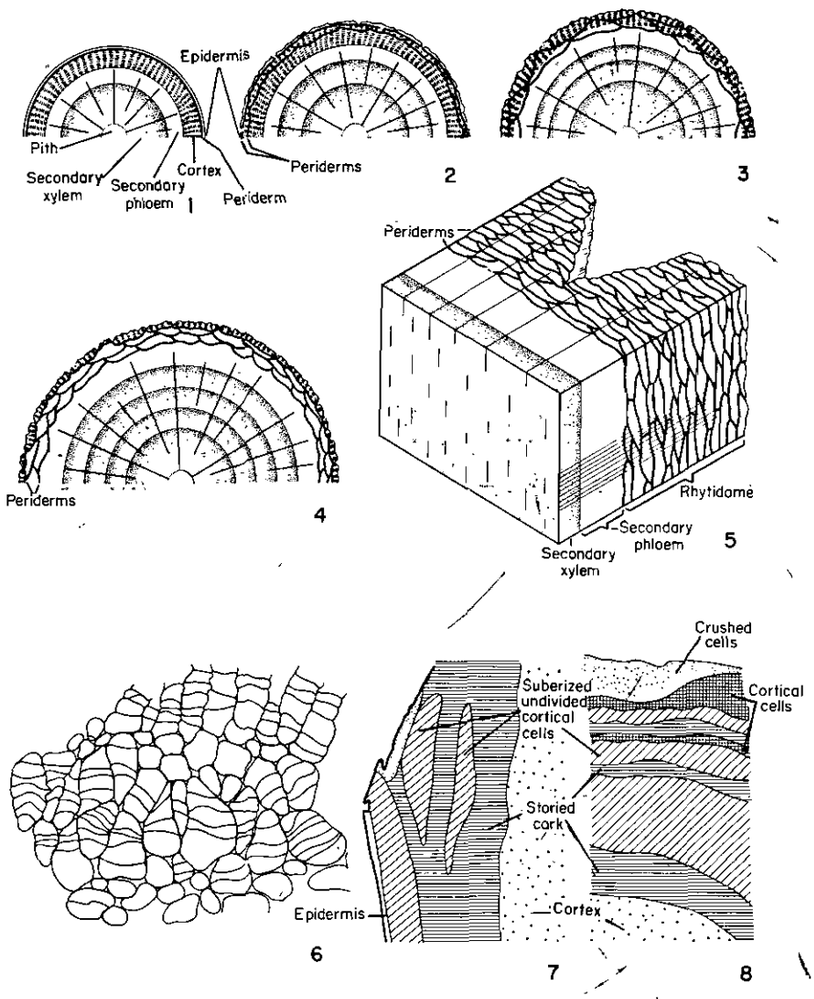

FIG. 150. 1–5, Diagrams showing the position, shape and extent of the additional periderms formed in a woody stem on which the first-formed periderm develops as an entire cylinder close to the epidermis. 1–4, As seen in cross-section of branches aged from 1–4, years. In nos. 3 and 4 the first-formed periderm together with the tissues external to it have sloughed away. 5, Three-dimensional diagram of an outer portion of a stem showing the peripheral tissues, which here include a narrow zone of functioning phloem and a wide rhytidome with deep grooves; a considerable amount of the latter tissue has been weathered away. 6–8, Protective layers of monocotyledons. 6, Cross-section of the outer part of the cortex of *Curcuma longa* showing storied cork. 7, Radial section of the stem of *Cordyline australis* showing the position of the layers of storied cork, which enclose patches of suberized undivided cortical cells. 8, Diagram of portion of a cross-section of the

crust increases in thickness due to the addition of further cork layers which enclose pockets of cortical tissue and dry phloem. All the cork layers together with the cortical and phloem tissues, external to the innermost phellogen, are termed *rhytidome* or *outer bark*; while all the tissues external

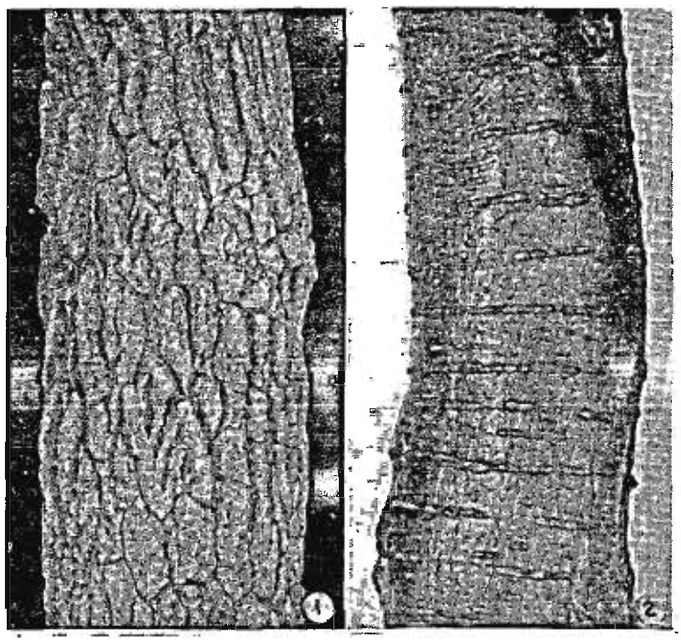

FIG. 151. 1, Photograph of a branch of *Calotropis procera* showing the deeply grooved rhytidome. ×0·6. 2, Branch of *Tamarix* sp. in which transverse lenticels can be seen. ×0·7.

to the vascular cambium are included in the term *bark*. The living part of the bark inside the rhytidome is often termed the *inner bark*. With the increase in diameter of the secondary xylem the circumference of the cambial cylinder enlarges. As a result of this, the new-formed layers of secondary xylem are larger in circumference than are the outer layers of the inner bark which are, therefore, brought under strain. This strain is accom-

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stem of *Cordyline indivisa* showing a superficial layer of crushed cells and alternating tangential bands of suberized, undivided cortical cells, and storied cork. (Nos. 1–5, adapted from Eames and MacDaniels, 1947; nos. 6–8, adapted from Philipp, 1923.)

modated by the production of *expansion tissue* and *proliferation tissue* (Whitmore, 1962a). Expansion tissue is an intercalary tissue formed mainly by the phloem rays (Fig. 147, no. 1), and proliferation tissue develops as a result of the proliferation of the axial phloem parenchyma.

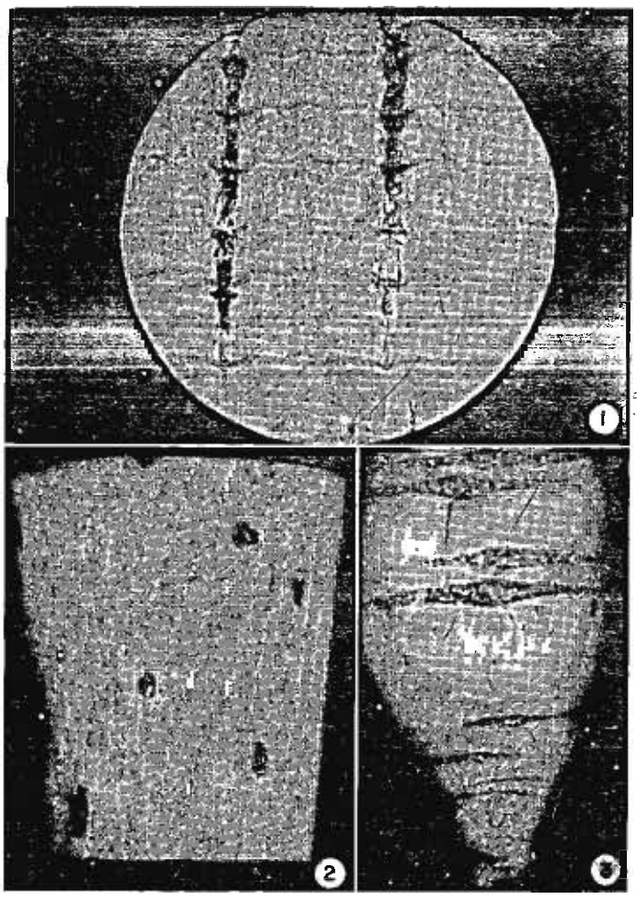

FIG. 152. 1 and 2. A bottle-stopper made of cork. 1. As seen from above (i.e. cross section of the cork relative to its position on the stem) in which wide growth rings and two lenticels can be seen. × 2·5. 2. As seen from the side (i.e. in tangential section of the cork relative to its position on the stem) in which the lenticels can be seen as dark patches. × 2·5. 3. *Raphanus sativus* root showing each lateral root to be accompanied by a pair of lenticels.

Morphology of bark

The outer appearance of stems differs in different species of plants and the type of bark is used in many cases as a taxonomic character. These differences result from the manner of growth of the periderm, the structure of the phellem and the nature and amount of tissues that are separated by the periderm from the stem. Therefore it is possible to conclude that the outer appearance of the stem is determined by the type of rhytidome.

In plants in which the first periderm forms close to the epidermis a small amount of primary tissue is cut off from the stem and is eventually shed. In this case the phellem becomes exposed and then no rhytidome is considered to be present on the stem. When such a phellem is thin its surface is usually smooth, while if it is thick, the surface is cracked and ridged. In plants where the first-formed periderm develops deep within the axis, thicker layers of tissue, which are usually connected to the cork, remain on the stem surface, and therefore these plants exhibit a rhytidome.

Certain rhytidomes, e.g. those of *Ulmus americana*, *Magnolia acuminata* and *Calotropis* (Fig. 151, no. 1), consist mainly of parenchyma tissue and soft phellem, while in others, e.g. species of *Quercus* and *Carya*, the rhytidome contains large quantities of fibres (mostly phloem fibres) which are associated with hard cork cells. The manner of formation of the periderm influences the shape of the bark in general and of the rhytidome in particular. When the subsequent periderms develop in the form of overlapping scales or shells the outer layers are sloughed accordingly, and so a *scaly bark* is formed. This type of bark occurs on relatively young stems of *Pinus*, *Pyrus communis* and others. In *Vitis*, *Lonicera*, *Clematis* and *Cupressus*, for example, the subsequent periderms are formed as entire cylinders and so the dead outer tissues are sloughed as hollow cylinders. This type of bark is termed *ring bark*. The bark of *Platanus*, *Arbutus* and species of *Eucalyptus*, for example, is intermediate between the above two types. In these plants the outer layers of the bark peel off in the form of relatively large sheets.

The sloughing of the outer layers of the bark is brought about in various ways. In *Arbutus* and *Platanus* the large plates of dead outer tissue separate from the inner portions of the bark through a layer of thin-walled cork cells, and the thick-walled cork cells below them remain attached to the stem which, therefore, has a smooth surface. In species of *Eucalyptus* the sheets of dead outer tissues of the bark exfoliate through layers of parenchyma cells with unthickened walls, which occur on the periphery of the phellem (Chattaway, 1953). In some trees, e.g. *Fagus*, the inner bark grows slowly and therefore much expansion tissue is formed. In this case the subsequent periderms cut off small amounts of secondary phloem and the sloughing of the outer bark is slow, resulting in the fall of minute scales and even powder (Whitmore, 1962b).

In many plants the different layers of the rhytidome adhere to one another and remain on the stem for many years and the outer bark becomes very thick and is deeply grooved. Such bark occurs in species of *Pinus*, *Quercus* and many other trees.

Commercial cork

Commercial cork is made from the bark of trees and, in particular, from that of *Quercus suber* (Eames and MacDaniels, 1947). In the stem of this plant the first phellogen forms in the epidermis. This phellogen may remain on the plant indefinitely but in order to obtain commercial cork this first-formed periderm is removed when the tree is about 20 years old and about 40 cm in diameter. After the first periderm is removed the exposed cells of the phelloderm and cortex dry out and die, and a new phellogen is formed a few millimetres within the cortex, below the first-formed phellogen. This subsequent phellogen produces cork more rapidly and in about 10 years a cork layer thick enough to be of commercial value is obtained. This cork is of better value than the virgin cork, which has almost no commercial value. However, it is of poorer quality than that of cork obtained from periderms that are formed as a result of subsequent strippings made at about 10 year intervals till the tree is about 150 or more years old. After a few strippings the phellogens are formed in the secondary phloem. The pieces of cork that are stripped from the tree exhibit surfaces with different structure—the outer surface is rough because of weathering and the presence of remnants of dead tissues outside of the phelloderm, while the inner surface is smooth. On the radial surfaces and in cross-sections of such pieces of cork, bands, which apparently represent annual increments, can be distinguished (Fig. 152, no. 1).

The dark brown spots that can be seen on tangential surfaces of cork and the similar stripes seen on radial surfaces and in cross-sections (Fig. 152, nos. 1, 2) are lenticels (see p. 344).

The features that give commercial value to cork are its imperviousness to gases and liquids and its strength, elasticity and lightness.

Protective tissues of monocotyledons

In herbaceous monocotyledons the epidermis, which has a cuticle, is the only means of external protection on the plant axis. When the epidermis is ruptured the cortical cells below become suberized. The suberin lamellae in these cells are laid down as in typical cork cells. This feature is common in the Gramineae, Juncaceae, Typhaceae, and other families.

Different types of protective tissues are found on the stems of perennial monocotyledons (Floresta, 1905; Philipp, 1923; Eames and MacDaniels,

1947; Tomlinson, 1961). For instance, in the palm *Roystonea*, in which the trunk is white and smooth, a hard periderm, which remains on the stem throughout the life of the plant, and which is similar to that of dicotyledons, is developed. According to the above authors, in thickened stems of the monocotyledons such as *Curcuma*, *Cordyline*, and many palms a special kind of protective tissue is developed. This tissue is formed by the secondary activity of a storied meristem which appears in the outer cortex. The initials of this meristem undergo three to eight periclinal divisions and so radially arranged layers of cells, which become suberized, are produced (Fig. 150, no. 6). Cork of this type is called *storied cork*. The initials here, unlike those of a typical phellogen, do not form a regular, uninterrupted cylinder.

The radial rows of cells that divide to form the storied cork are arranged in irregular tangential bands which enclose between them large cells which do not divide but which, however, are also suberized. The individual bands of storied cork may fuse both radially and tangentially (Fig. 150, nos. 7,8). The layers of storied cork may be formed further in towards the centre of the trunk and between these layers alternating layers of undivided suberized cells and non-suberized destroyed cells occur (Fig. 150, no. 8). In this way layers that are analogous to, but less organized than, the rhytidome of dicotyledons are formed.

From observations made on *Dracaena* sp., *Aloë arborescens* and *Yucca*, it was found difficult to detect differences between the secondary protective tissues developed in them and those of dicotyledons which are produced by a typical phellogen.

Wound cork

Generally, in such places where living plant tissue is exposed to the air as a result of wounding *wound cork* is developed. Usually the outer dead tissues are separated from the inner intact ones by a layer of cells which become suberized. Apart from this separating layer a phellogen may be developed in the living undamaged layers. This phellogen produces phelloderm and phellem in the usual manner. The layer of cork thus formed prevents the loss of water through the wound and it protects the plants against the entry of fungi and bacteria. Apparently wound cork may develop on all parts of the plant, including even fruits and leaves. However, there are differences in the type and amount of cork developed in different species, organs and tissues, and under different environmental conditions. Usually wound cork is more easily developed on woody plants than on herbaceous or monocotyledonous ones. Low temperatures and low humidity may delay the development of wound cork even in those places where it develops readily as, for example, on potato tubers (Küster, 1925; Artschwager and Starrett, 1933; Bloch, 1941).

Polyderm

In certain species of the Rosaceae, Myrtaceae, Hypericaceae and Onagraceae, a special phellogen is formed in the pericycle of the root or underground stem. This phellogen produces, centrifugally, a few layers of thin-walled non-suberized cells which alternate with a layer of endodermal-like cells. At the start of the differentiation of the latter into cork cells, Casparian strips appear on the walls, which, with further development, become entirely lined by a suberin layer. This type of complex tissue is termed *polyderm*. Its inner layers, including the cork cells, are living and may serve as a storage tissue (Mylius, 1913; Luhan, 1955; Nelson and Wilhelm, 1957).

Lenticels

In the large majority of plants there are restricted areas of relatively loosely arranged cells, suberized or non-suberized, in the periderm. These areas are termed *lenticels*. Lenticels protrude above the surrounding periderm because of the bigger size and loose arrangement of the cells which, themselves, are usually more numerous in these regions. Because of the continuity of the intercellular spaces of the lenticels and those of the inner tissues of the axial organ, it is assumed that the function of the lenticels is connected with gas exchange, similar to that of the stomata on organs covered by an epidermis only.

DISTRIBUTION OF LENTICELS

Lenticels usually occur on stems and roots, and they appear on young branches and other smooth organs as rough, dark patches which are somewhat raised above the epidermis through which they erupt (Fig. 151, no. 2). Lenticels are also sometimes present on fruits. In apples and pears, for example, they appear as small dots on the surface of the fruit. Only a few plants, e.g. *Philadelphus*, *Anabasis*, *Haloxylon*, *Campsis radicans*, *Vitis*, and some other species, many of which are climbers, do not possess lenticels although they form a periderm.

The number of lenticels occurring on a unit of surface area of a stem differs in the various species (Eames and MacDaniels, 1947). In certain species a lenticel develops under each stoma, or under a group of stomata. In others, lenticels may also develop between stomata if the latter are sparsely distributed, and, if the stomata are very numerous, lenticels may develop only under some of them. The arrangement of the lenticels on the stem also varies—sometimes they appear in longitudinal or horizontal rows, but generally they are irregularly scattered over the entire surface. In

young roots the lenticels usually appear in pairs—one lenticel on each side of a lateral root (Fig. 152, no. 3). In storage roots, such as those of *Daucus*, for example, the pairs of lenticels appear in vertical rows alongside the rows of lateral roots. In older roots the arrangement of the lenticels is irregular.

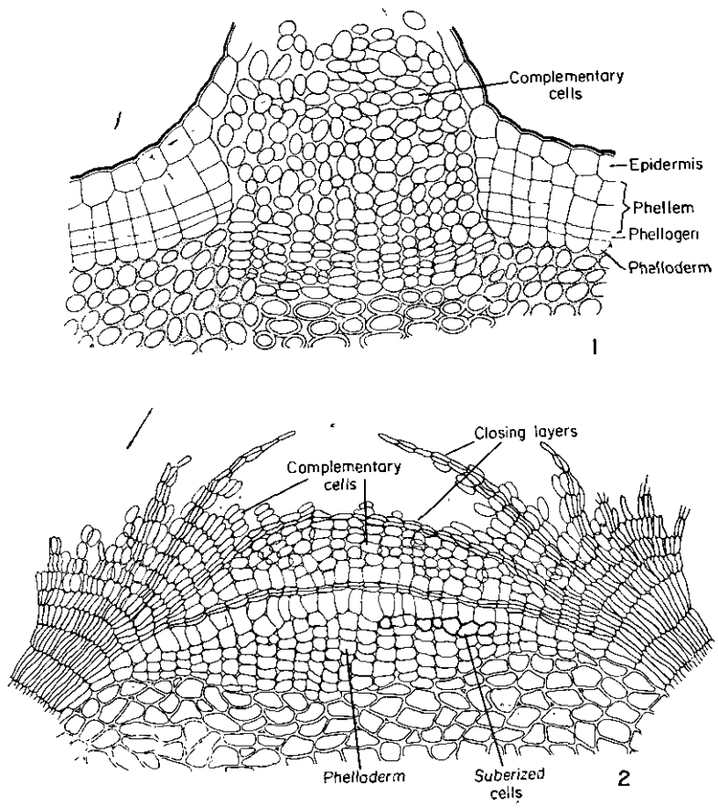

FIG. 153. 1, Young lenticel of *Sambucus nigra*. 2, Mature lenticel of *Prunus avium*. (No. 1 adapted from Troll, 1948; no. 2, adapted from Boureau, 1954.)

Externally mature lenticels are usually lens-shaped and they are convex both towards the exterior and the interior (Fig. 153, no. 2). According to the orientation of the rupture of the epidermis the lenticels are described as being longitudinal or transverse (Fig. 151, no. 2). The lenticels which are situated close to the outer ends of the phloem rays enable relatively free passage of gases between the inner tissues of the axis and the atmosphere.

In stems with larger vascular rays it may be seen that the lenticels usually appear directly opposite the rays.

In the roots of *Phoenix dactylifera* lenticellular structures occur which take part in aeration of the root but which differ from the above-described ordinary lenticels. Here the lenticels form collar-like structures around the thinner roots. The complementary tissue is, however, of typical structure.

DEVELOPMENT AND STRUCTURE OF LENTICELS

Lenticels begin to form together with the first periderm or shortly before. The time of the formation of the lenticels differs in various species and it is dependent on the persistence of the epidermis on the stem. In most species the development of the lenticels is already commenced during the first season of growth of the organ and sometimes even before the elongation or the organ is completed.

The first-formed lenticels generally appear below a stoma or group of stomata. The cells in these regions begin to divide in different directions and the chlorophyll in them disappears so that a loose colourless tissue is formed. The division of the cells progresses in the cortex inwards and the orientation of the divisions becomes more and more periclinal until the phellogen of the lenticel is formed. The cells that are derived from the divisions of the substomatal cells, as well as those produced towards the exterior by the phellogen of the lenticel, are termed *complementary cells.* The increase in number of these cells causes the rupture of the epidermis so that masses of complementary cells are pushed out and rise above the surface of the organ. The exposed cells die and weather away and they are replaced by new cells produced by the phellogen (Fig. 153, no. 1). Complementary cells may be suberized or non-suberized, and they are usually more or less spherical and thin-walled. Centripetally the phellogen of the lenticel may produce phelloderm.

In some species, apart from the complementary cells, the phellogen of the lenticel also produces *closing layers* centrifugally (Fig. 153, no. 2). These layers, which consist of compact tissue, alternate with the complementary tissue.

Two types of complementary tissue are distinguished: that in which the connection between the cells is relatively strong, as, for example, in *Sambucus* (Fig. 154), *Salix* and *Ginkgo;* and that in which the cells have almost no attachment between them giving the tissue a powder-like appearance, as, for example, in the stems of *Pyrus*, *Prunus* and *Robinia* and in the roots of *Morus* (Eames and MacDaniels, 1947). In the latter type the cells of the complementary tissue are held in place by the closing layers (Fig. 153, no. 2). In spite of their compactness, the closing layers contain intercellular spaces which allow the passage of gases. Similar gaps are found in the

phellogen itself. The closing layers are ruptured as a result of the continual production of new complementary cells. In the temperate zones the lenti-

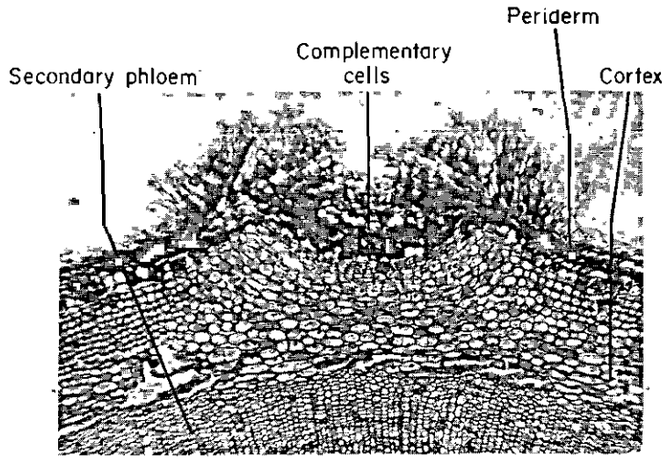

FIG. 154. Micrograph of a cross-section of a lenticel of *Sambucus nigra*. ×50.

cels become closed at the end of the growing season by a closing layer. This layer is ruptured only with the renewal of the activity of the plant which is accompanied by the rapid and excessive production of new complementary cells.

DURATION OF LENTICELS

In plants in which additional inner periderms are formed relatively early in the life of the plant, the lenticels are cut off early from the inner tissues and are shed together with the outer tissues of the bark. In plants in which the first-formed outer periderm remains for a long time on the axial organ, the lenticels may remain active for many years. In these cases the lenticels elongate transversely as a result of secondary growth. The elongation of the phellogen of the lenticel in a tangential direction, with the increase of the circumference of the organ, is brought about by anticlinal divisions of the initials as occurs in the phellogen surrounding the lenticel. On the stems of some plants, e.g. *Acacia raddiana*, *Tamarix gallica* and *Betula*, and on the roots of *Morus*, for example, the transversly elongated lenticels form conspicuous marks on the surface of the smooth bark. In some plants the lenticels do not increase in size with age, but they become split into several lenticels. In certain plants, e.g. *Quercus suber* and *Ailanthus*, there is no appreciable increase in size of the lenticels with age.

In the subsequent periderms new lenticels are produced as a result of the activity of special areas of the new phellogens. In plants with rough barks the lenticels are not easily seen as they occur in the additional inner periderms at the base of the cracks in the outer bark. These cracks are a result of the continued secondary growth.

In *Quercus suber*, where the cork layer is several centimetres thick, the lenticels remain active for a long time and result in the formation of cylinders of complementary tissue (Fig. 152, nos. 1, 2) which extend from the phellogen to the surface of the phellem. This complementary tissue forms the patches of dark brown crumbling tissue found in commercial cork. Because of the radial orientation of these cylindrical masses of complementary tissue, bottle corks are cut from the cork tissue in a direction parallel to the surface of the trunk so that the cylindrical lenticels extend transversely through them.

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CHAPTER 18

ANOMALOUS SECONDARY GROWTH

THE usual structure of the secondary conducting tissues of most spermatophytes is as has been described in the previous chapters. The processes of secondary growth that give rise to this type of structure may be termed the *common type of secondary growth.* However, in many plants there are deviations from this type of secondary growth. Such deviations may include such features as the unequal activity of different portions of the cambium on the circumference of the axis, the alteration of the relative amounts and position of the xylem and phloem, and the appearance of additional cambia. The secondary growth that results in the development of a secondary body differing from the common is termed *anomalous secondary growth.*

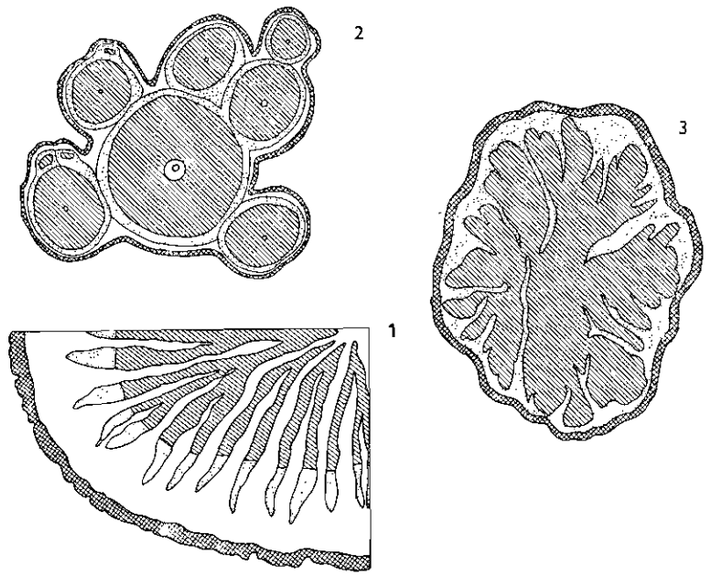

FIG. 155. Diagrams of cross-sections of stems with anomalous secondary thickening. 1, *Aristolochia triangularis*, portion of a cross-section. 2, *Serjania clematidifolia.* 3, *Heteropteris anomala.* Periderm—cross-hatched; secondary phloem—stippled; secondary xylem—hatched. (No. 1, adapted from Schenk, 1892; nos. 2 and 3, adapted from Pfeiffer, 1926.)

If, ina cross-section of a stem, the cambium produces more xylem than phloem in certain places and more phloem than xylem in others, the xylem cylinder becomes ridged and sometimes even much more complex structures may develop (Fig. 155, no. 3). In certain plants such as *Aristolochia*, for example, there are strands of cambium that produce only ray-like paren-

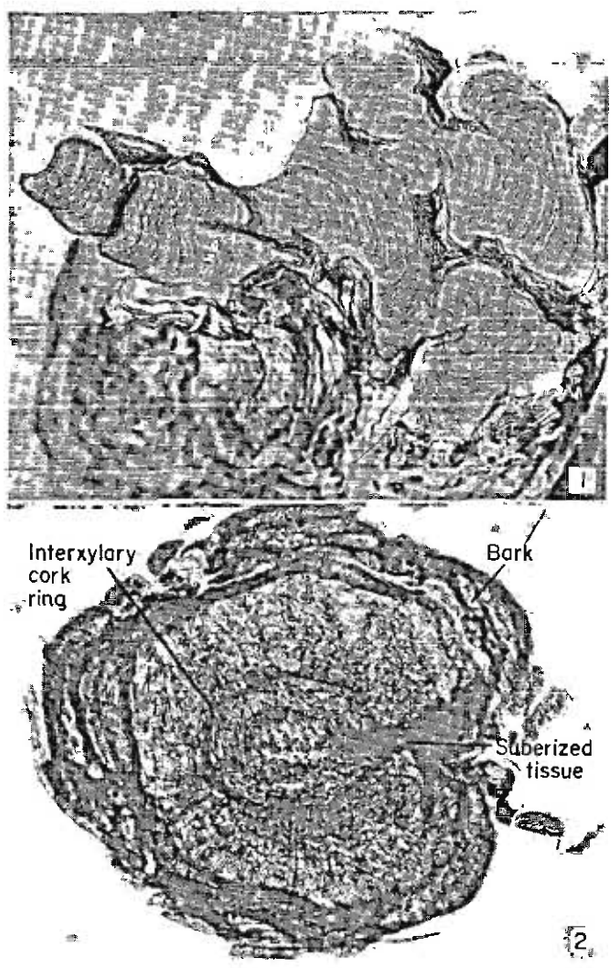

FIG. 156. 1, Surface view of a cross-section of the stem of *Zygophyllum dumosum* showing the splitting that results from the cessation of cambial activity in localized areas. ×0.8. 2, As above but of a 2-year-old stem of *Artemisia herba-alba* showing an interxylary cork ring and suberized tissue which splits the last growth ring. ×16.

chyma; these strands increase in number with the increase of the circumference of the cambium (Fig. 155, no. 1). The reduction of the activity of the cambium to restricted areas only results in the formation of ridged stems, which often split. The latter type of secondary growth occurs in *Peganum harmala* and *Zygophyllum dumosum* (Fig. 156, no. 1), among others. In certain genera, for instance, *Serjania*, of the Sapindaceae, the cambium first appears in separate strands each of which surrounds a group of vascular bundles or even a single primary vascular bundle (Fig. 155, no. 2). Stems that develop in this way appear as if they originate from the fusion of a number of stems. With the aging of such stems and with the production of periderm layers the stems split into numerous parts (splits). A similar structure can result from the excessive development of the xylem and phloem parenchyma which results in the splitting of both the conducting tissues and the cambium cylinder.

In *Achillea fragrantissima* and some species of *Artemisia* a layer of cork is produced each year on the border between two growth rings of xylem, i.e. *interxylary cork*. This feature, when accompanied by the suberization of the rays, as in *Artemisia herba-alba*, for example (Ginzburg, 1963), or by the cessation of activity in certain portions of the cambium, also results in the splitting of the stem (Fig. 156, no. 2).

Included phloem

In certain plants strands of secondary phloem develop within the secondary xylem. In genera such as *Strychnos* (Loganiaceae), *Leptadenia* (Asclepiadaceae), *Thunbergia* (Acanthaceae), *Bougainvillea* (Nyctaginaceae), *Salvadora* (Salvadoraceae), and in various species of the Amaranthaceae, Chenopodiaceae and other families, strands of secondary phloem become included in the following way. Strips of the cambium cease to function and the cells in these strips undergo differentiation to form conducting tissues. New strands of vascular cambium later develop, by redifferentiation, in the outer phloem parenchyma produced by these strips. The margins of the new cambial strands connect up with the rest of the cambium which continues to function in the usual manner. In this way xylem is produced on the outside of the phloem strand, which therefore becomes included within the xylem. This type of activity is repeated many times so that secondary xylem with scattered groups of included phloem (Fig. 158, nos. 1–3; Fig. 159, no. 1) is produced (Pfeiffer, 1926; Iljin, 1950).

In the Chenopodiaceae the additional cambia are, as seen in cross-section, in the form of long or short arches. They appear irregularly or spirally in the phloem or outside it (Fig. 157, no. 1). Frequently the additional cambia in this family form more or less entire rings (Fig. 157, no. 2). Sometimes an ontogenetic relationship exists between the successive cam-

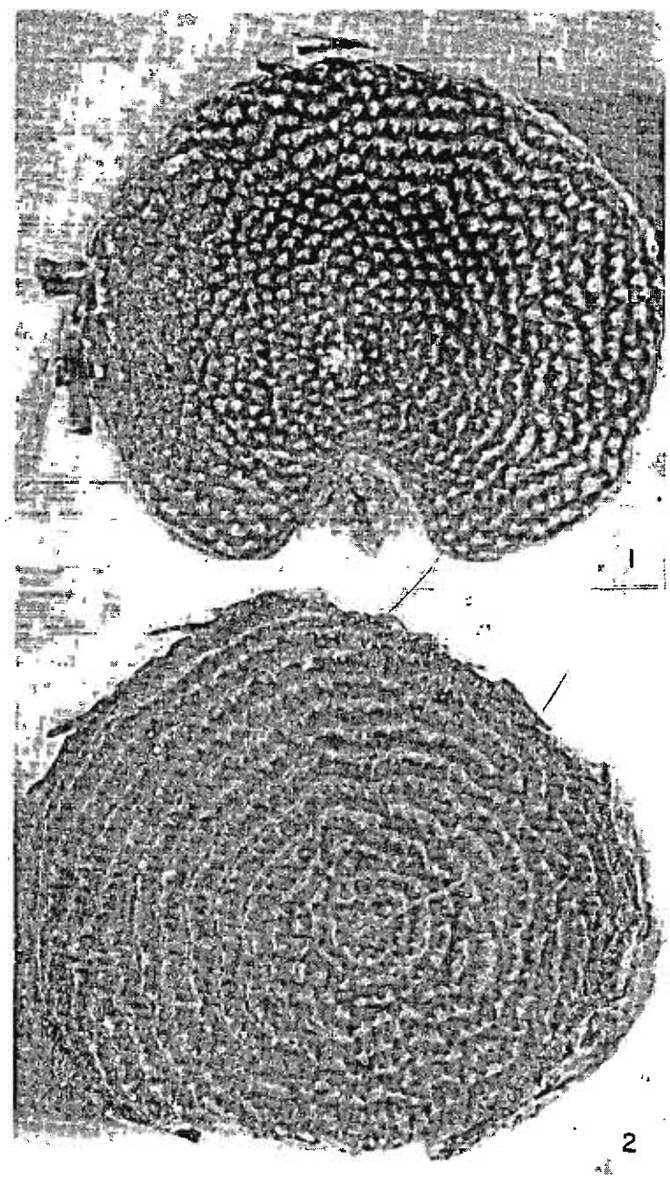

FIG. 157. Surface view of cross-sectioned stems of plants belonging to the Chenopodiaceae showing different arrangements of the included phloem and its associated tracheary elements. 1, *Haloxylon articulatum*. ×10. 2, *Anabasis articulata*. ×6.

bia, as is the case in *Beta*, for example (Artschwager, 1926). The cambial initials divide and the inner cells resulting from this division continue to divide a number of times before they undergo differentiation into xylem and phloem elements, while the outer cells form the initials of the next outer cambium, which replaces the former one. The initials of this cambium

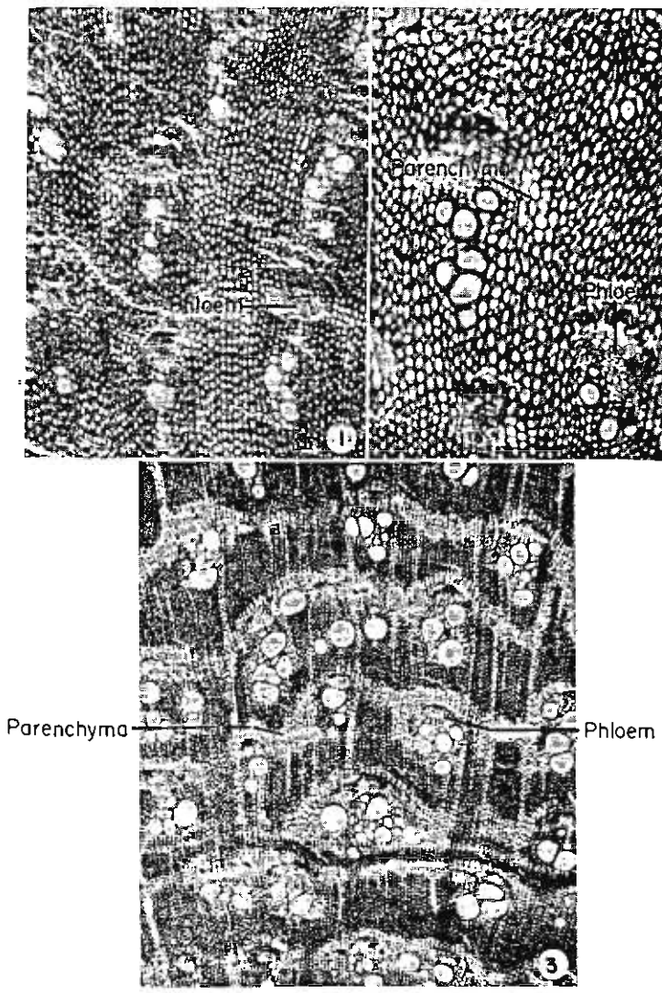

FIG. 158. Micrographs of cross-sections of secondary xylem with included phloem. 1, *Atriplex halimus*. ×105. 2, *A. portulaccoides*. ×135. 3, *Bougainvillea glabra*. ×34

divide similarly to those of the cambium which it replaces, and this feature is repeated many times.

In some species, e.g. *Salvadora persica* (Singh, 1944; and some earlier authors), *Thunbergia mysorensis* and *T. grandiflora* (Mullenders, 1947), no additional cambia are formed. The included phloem is differentiated from localized patches of thin-walled cells which are produced centripetally by the normal cambium. Subsequently the cambium resumes normal activity i.e. the centripetal production of xylem, in these regions. As a result of this the above-mentioned patches of phloem become deeply embedded in the secondary xylem (see also: Structure of storage roots, p. 258).

In many species of the Chenopodiaceae, in *Bougainvillea* and in other plants with similar secondary thickening, each strand of secondary phloem is accompanied, on its inner surface, by a group of xylem vessels (Fig. 158, nos. 1–3). In cross-section such stems appear, therefore, to consist of a fibrous ground tissue in which there are scattered "vascular bundles". The parenchyma associated with the included phloem is termed *conjunctive tissue*. This parenchyma is variously arranged and developed: it may be ray-like or in bands that connect the phloem strands, or it may surround and intermingle with the vessel groups. The phloem strands and vessels of these "vascular bundles" of the secondary body may anastomose both tangentially and radially, but tangential connections are the more common.

In the perennial species of the Chenopodiaceae growing in the desert the anastomosing system of included phloem may have important adaptive value, especially as the phloem in this family may remain active for many years. Even in cases where the outer tissues of the stem dry out during the long summer, the included phloem strands remain viable and so can supply nutrients to the buds which, at the onset of the growing season, can then commence to develop.

Secondary growth in monocotyledons

In most monocotyledons secondary thickening is absent, but in those plants that have thick axial organs, e.g. the stems of palms, the rhizomes of *Musa* spp. (Fig. 160, no. 3) and *Veratrum album* and the bulbs of *Galanthus nivalis* and *Tulipa*, much and rapid thickening takes place below the apical meristem (Skutch, 1932; Ball, 1941; Clowes, 1961). This thickening is accomplished by a *primary thickening meristem*. The activity of this type of meristem is somewhat similar to that of a vascular cambium and if these two types of tissue occur in one and the same plant then the latter develops from the former. Ball (1941) described the primary thickening meristem and its activity in the Palmae in the following way. During the process of growth of the stem, the activity of the primary thickening meristem is largely independent of the apical meristem (Fig. 159, no. 2). In the

embryo the primary thickening meristem constitutes a flat zone below the leaf and sheath primordia and, in the seedling, a steep cone. In later stages of development this meristem again appears as a flat zone and eventually it becomes concave. Most of the stem tissues develop from it. During the maturation of the palm the primary thickening meristem at first contributes mainly to the thickening of the stem, but later it is also responsible

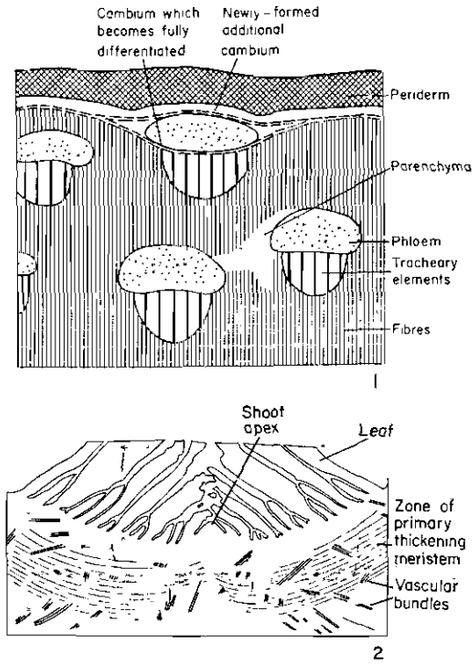

FIG. 159. 1, *Diagram of portion of a cross-section of a stem with* anomalous secondary thickening illustrating how the strands of included phloem are formed. 2, Diagram of a median longitudinal section of the shoot apex of *Washingtonia filifera*. (No. 2, adapted from a micrograph of Ball, 1941.)

for the increase in stem height. Below the concave meristematic zone of the mature palm longitudinally orientated rows of cells can be distinguished; the activity of this zone results in the increased length of the trunk. The primary thickening meristem develops as the result of periclinal divisions in the cells in the region below the very young leaf and sheath primordia. This meristem has no special layer of initials, such as is present in a typical vascular cambium. In the banana corm new cells are added to the primary thickening meristem from the cortex.

In the palms and in the banana corm the provascular strands (the procambium) are derived from two sources—to a smaller extent from the shoot apex, and to a larger extent from the primary thickening meristem.

In addition to the above-mentioned meristem which brings about primary thickening, in palm stems the ground tissue close to the apex expands and thus also results in additional thickening of the stem. It has been reported (Zodda, 1904; Schoute, 1912; Tomlinson, 1961) that in some palms the expansion of the ground tissue continues for a long period and that it is very obvious in the older parts of the stem which are considerably distant from the shoot apex (e.g. in *Roystonea* and *Actinophloeus*). Here the central parenchyma cells and the not yet fully differentiated outer fibres of the bundle sheath continue to undergo divisions, which are followed by cell expansion, for a long period. The intercellular spaces also increase in size proportionally to the increase in size of the parenchyma cells. This type of secondary thickening has been termed *diffuse secondary growth* (Tomlinson, 1961). The ventricose shape of some palm trees is, according to Tomlinson, probably due to the increased vigour of the leafy crown, and such stems are mainly of primary origin, but some secondary thickening may also take place.

Secondary thickening proper takes place in different monocotyledonous species such as *Aloë arborescens*, species of *Yucca*, *Dracaena* and *Sansevieria* of the Liliaceae, species of *Agave* of the Amaryllidaceae, and in species of *Xanthorrhoea*, *Kingia* and *Lomandra* of the Australian family, the Xanthorrhoeaceae (Cheadle, 1937; Fahn, 1954). Secondary thickening in the monocotyledons is brought about by a special cambium which appears in that part of the stem that has already ceased to elongate and which is in continuation with the primary thickening meristem (Chouard, 1937). This cambium develops in the parenchyma of the stem external to the entire mass of primary vascular bundles. The cells of this secondary meristem are, as seen in tangential view, of different shapes—they may be fusiform (that is, long with tapered ends), rectangular, or with one tapered and one truncate end.

The monocotyledonous cambium functions in the manner described below. At first the initials of the cambium produce cells towards the centre of the stem and only later a small amount of tissue is produced toward the circumference. The cells produced on the outside of the cambium all develop into parenchyma cells, while those produced on the inside develop, in part, into parenchyma and, in part, into the vascular bundles (Fig. 160, nos. 1,2). The inner parenchymatous ground tissue is termed *conjunctive tissue* and the walls of its cells may sometimes become thickened. The bundles develop from single cells that are cut off from the cambial initials. Each of these single cells represents the centre of a future vascular strand. These cells divide anticlinally to produce two or three rows of cells which then divide periclinally; later the direction of the divisions becomes hap-

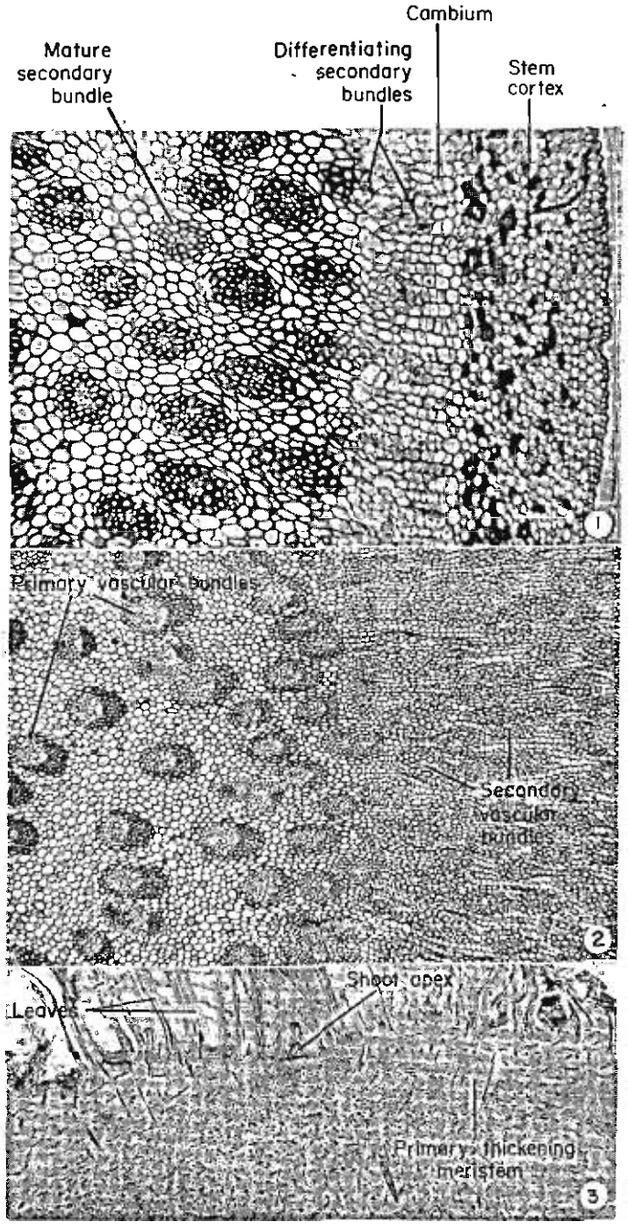

FIG. 160. 1 and 2, Portions of cross-sections of monocotyledonous stems showing the type of secondary growth characteristic in this group. 1, *Aloë arborescens.* ×48. 2, *Dracaena.* ×32. 3, Upper portion of a median longitudinal section of the vegetative shoot apex of *Musa* (Dwarf Cavendish banana) in which the zone of the primary thickening meristem can be distinguished. ×3.

hazard but still longitudinal. In this manner the secondary vascular bundles are formed. The cells of the bundle undergo sliding growth during their development. The xylem elements elongate fifteen to forty times their original length, while the xylem parenchyma and the phloem elements undergo little or no elongation. The thickening of the walls of those tracheids closest to the centre of the axis commences, in most cases, prior to the completion of the cell division in the developing bundle (Cheadle, 1937).

The secondary bundles may be amphivasal, i.e. the xylem surrounds the phloem as is seen in *Xanthorrhoea*, *Lomandra*, *Dracaena* (Fig. 83, no.3) and *Aloë arborescens*, for example, or the xylem may surround the phloem on three sides and then the bundle appears U-shaped in cross-section as is seen, for example, in *Kingia* (Fig. 72, no. 1). The tracheary elements of these bundles in all the species that have as yet been studied are all tracheids. The walls of the parenchyma cells in which the vascular bundles are scattered may be thin or thick and lignified. The parenchyma that develops externally to the cambium usually remains thin walled and in many plants many of the cells of this tissue contain crystals. In *Xanthorrhoea* resin is secreted in the cells of the outer parenchyma so that a resin sheath is formed around the stem. (It is reported that the aborigines of Australia have almost completely destroyed the trees of *Xanthorrhoea* by burning them in order to enjoy the beautiful flames that result from the burning of this resin sheath.)

The connection between the primary and secondary bodies in monocotyledons with secondary thickening is strong, as it is in the dicotyledons. The union, in monocotyledons, is even more obvious because there are connections between the secondary bundles and the peripheral foliar ones.

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REPRODUCTIVE ORGANS

CHAPTER 19

THE FLOWER

Floral organs

The problem of homology and morphological evolution of the flower has occupied research workers for a long time. Investigators such as Wolff and Goethe in the eighteenth century and De Candolle at the beginning of the nineteenth century, and many others since then, were interested by this problem (Arber, 1937, 1950). Opinions were expressed that floral organs are derived directly from foliage leaves. However, in the light of the view generally accepted today that the leaves and stem constitute a single unit which is termed the shoot, we can visualize the development of the flower as being parallel to that of a vegetative branch and not as being derived from it.

The flower consists of an axis on which the rest of the floral organs are borne. That part of the axis that represents the internode terminated by the flower is termed the *pedicel*. The distal end of the pedicel is swollen to various extents and this portion is termed the *floral receptacle* or *thalamus*. The floral organs are attached to the receptacle. A typical flower has four types of organs. The outermost organs of the flower are the *sepals*, which together constitute the *calyx* which is usually green and is found lowest on the receptacle. On the inside of the sepals is the *corolla*, consisting of the *petals* which are generally coloured. These two types of organs together form the *perianth*; however, sometimes one of them may be lacking. When all the organs of the perianth are similar they are termed *tepals*. Within the perianth two kinds of reproductive organs are found: externally the *stamens* which together form the *androecium*, and internally the *carpels* which form the *gynoecium*.

The arrangement of the floral organs on the receptacle may be spiral or whorled, and both types of arrangement may occur in the same flower. In most flowers in which the arrangement is whorled, the organs of each whorl alternate with those of the neighbouring whorl. The floral organs may be *free* or fused. Fusion of organs of the same type is termed *cohesion*, and that of different types of organs, *adnation*.

The term *pistil* is no longer used as it is not sufficiently well defined. This term was used both for each of the free carpels of a flower as well as for the unit which is formed by the fusion of a few carpels. Therefore, in this book we shall refer to all the carpels of a flower, whether they are free or fused, as the gynoecium.

The stamen consists of a *filament* which distally bears the *anther*. Two lobes can be distinguished in the anther and they are attached to a continuation of the filament which is termed the *connective*. Each of these lobes contains two *pollen sacs* in which *pollen grains* are found. The pollen grains in their early stage of development are the microspores of the angiosperms.

The free carpei or fused gynoecium usually consists of the following three parts: the *ovary*, a hollow body which contains one or more *ovules*; the *style* which results from the elongation of the ovary wall; and the *stigma* which is that part at the top of the style which has a surface structure enabling pollination. The ovules are attached to a special thickened region of the carpel wall which is termed the *placenta*.

When the carpels are found on the highest level of the floral axis the ovary is termed *superior* and the flower, *hypogynous*. In certain plants the perianth and stamens are located on the edge of a laterally expanded disc which raises them above the ovary; such a flower is termed *perigynous*, and its ovary is said to be *intermediate* or *pseudo-inferior*. The concave disc may completely enclose the ovary so that it is then found below the other floral organs; in such a flower the ovary is said to be *inferior*, and the flower *epigynous*.

In some plants, e.g. *Capparis*, only that part of the receptacle that bears carpels is elongated; such a structure is termed a *gynophore*. An elongation of that part of the receptacle that bears the carpels and stamens, e.g. *Passiflora*, is termed *androgynophore*.

Ontogeny of the flower

The morphological changes that take place when a vegetative apex becomes reproductive are usually rapid and obvious. In many plants the axis elongates abruptly during this time or immediately afterwards and the apex widens and often becomes slightly flattened (Popham and Chan, 1952; Fahn *et al.*, 1963). The sudden elongation of the flower-bearing axis prior to flowering is especially noticeable in those plants in which the internodes are very short and in which the foliage leaves form basal rossettes, e.g. in many species of the Compositae, in the Gramineae, and in the banana (Skutch, 1932; Barnard, 1957, and others). The elongated axis may bear a single flower but usually it bears an inflorescence. The terminal meristem and the meristems in the axils of the bracts may develop flowers in the order (Fig. 161, nos. 1–4) that reflects the type of inflores-

cence (Fahn, 1953a). In a vegetative apex the apical meristem usually continues to function above the developing leaf primordia, but in the case of a developing flower the meristematic zone in the apex diminishes until it is lost completely, or until a small, non-active residue alone remains (Tepfer, 1953; Leroy, 1955).

As has already been mentioned in Chapter 3, the arrangement of the cells in the apical meristem alters when the shoot apex changes from the vegetative stage to the reproductive. In the apical meristem of the inflorescences and of the individual flowers of most plants that have been examined, a central zone of cells with large vacuoles has been observed to be covered

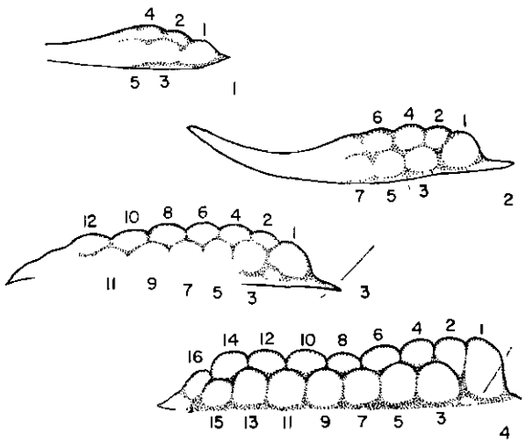


FIG. 161. Four stages in the ontogeny of a flower cluster of *Musa*; the numerals indicate the order of the appearance of the floral primordia.

by a zone of relatively small cells which are rich in protoplasm and which mostly divide anticlinally. With this development the activity of the rib meristem ceases. It will not be discussed here whether in the reproductive apex a tunica-corpus arrangement is present, but it should be mentioned that the number of cell layers in the outer zone is usually larger than that found in the vegetative apex. The initiation and the first stages of histological differentiation of the different floral organs are, in principle, similar to the early ontogenetic stages of bracts and foliage leaves (Tepfer, 1953).

The morphological and functional differences between the different floral organs are apparently related to a series of physiological processes which take place during the different stages of floral differentiation. This assumption is supported by the results of experiments which involved the incising and dissecting of the primordia of floral organs at different developmental stages (Cusick, 1956).

The developing floral organs usually appear in a distinct acropetal order

(Fig. 162, nos. 1, 2), i.e. the youngest organs are closest to the apex. However, in certain genera and families; e.g. *Paeonia*, the Bixaceae, Dilleniaceae and Tiliaceae, the floral apex stops growing and then basipetal or

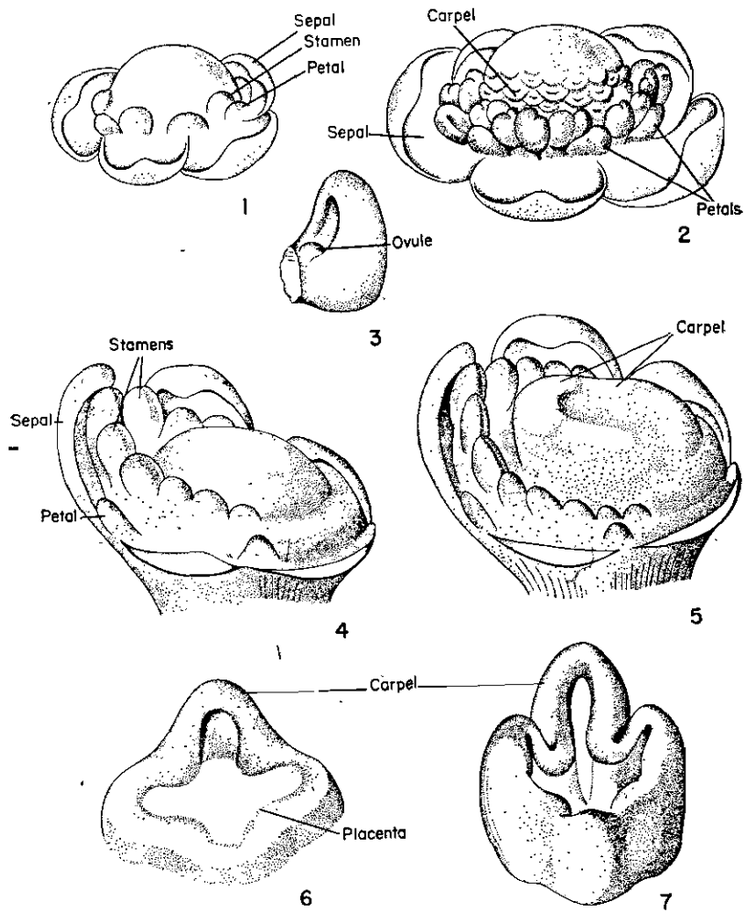


FIG. 162. Ontogeny of flowers. 1–3, *Ranunculus trilobus*. 1 and 2, Two stages in the development of the entire flower. 3, Developing carpel. 4–7, *Reseda odorata*. 4 and 5, Two stages in the development of the entire flower. 6 and 7, Developing gynoecium at stages later than those depicted in nos. 4 and 5. (Adapted from Payer, 1857.)

centrifugal development of the staminal primordia can be distinguished in the zone of the stamens (Corner, 1946; Sporne, 1958). Other deviations from the usual ontogenetic development of the floral organs are also known.

Sometimes there may be a delay in the development of the petals although their primordia appear prior to those of the outermost stamens. In zygomorphic flowers unequal development of the floral organs is already obvious in early ontogenetical stages. In *Reseda*, for example (Fig. 162, nos. 4, 5), the adaxial side of the receptacle is already better developed than the abaxial side in the earliest stage of development, and the abaxial petal appears only after the adaxial stamens are almost fully developed.

In those flowers in which certain organs are partially reduced, as, for instance, in the case of the sterility of some of the stamens, the development of these organs is retarded in relation to that of the other normal organs.

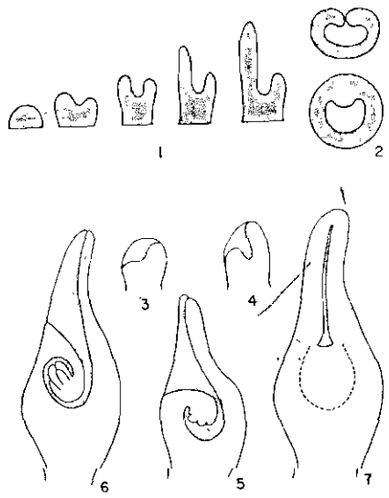


FIG. 163. Development of a peltate carpel in an apocarpous gynoecium. 1 and 2, Diagrams of sections of the carpel at different ontogenetic stages. 1, Longitudinal sections. 2, Cross-sections. 3–7, Different stages in the development of the carpel in *Thalictrum* showing the development of the sill, the ovule and the portion above the sill which folds over and closes the locule. 3–6, Developing carpel sectioned longitudinally. 7, Surface view of the side of the carpel on which the closure took place. (Nos. 1 and 2, adapted from Goebel; nos. 3–7, adapted from Troll.)

The development of the reduced organs ceases completely before mature shape is obtained. The female flower of *Musa* may be given as an example of such development. In certain species the appearance of primordia of reduced organs may be retarded in relation to that of the similar normal organs. Examples also exist in which the carpels mature before the stamens. This feature is apparently brought about by a local concentration of growth substances (McLean and Ivimey-Cook, 1956).

In flowers in which the gynoecium is *apocarpous*, i.e. in which the carpels are free, each carpel primordium appears in its earliest stage of develop-

ment as a rounded buttress which is similar to the primordia of the other floral organs and leaves. In a later stage of development the carpel primordium resembles that of a peltate leaf (Fig. 163, nos. 1–7). Still later

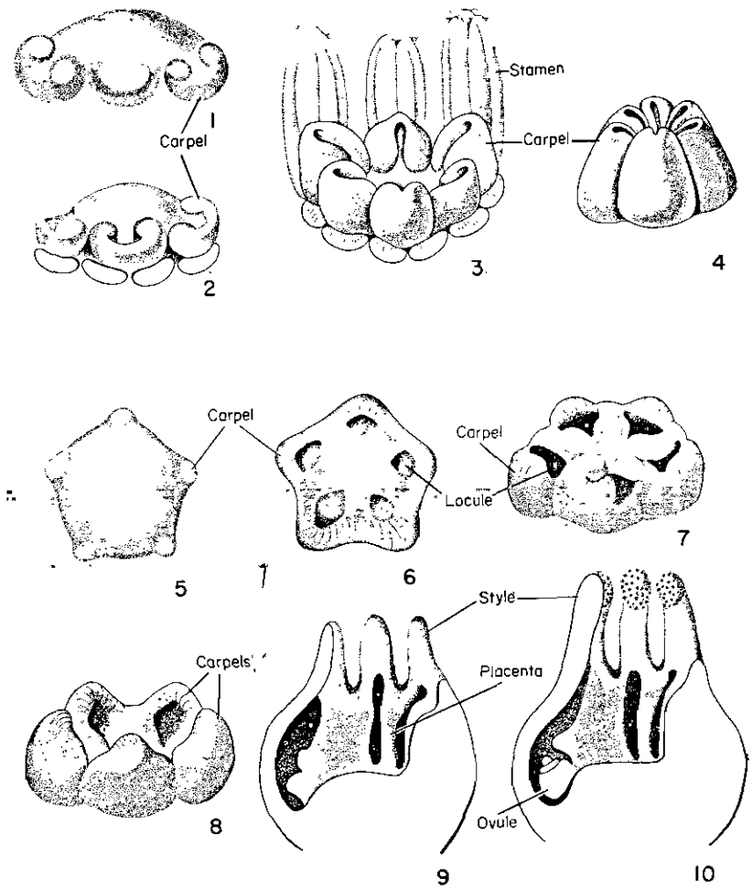


FIG. 164. Ontogeny of flowers. 1–4, Development of the apocarpous gynoecium of *Butomus umbellatus*. 5–10, *Linum perenne*. Stages in the development of the syncarpous gynoecium from separate primordia which expand laterally and fuse to form a single ring. (Adapted from Payer, 1857.)

a depression appears at the tip of the primordium and as a result of unequal development, which then commences, an abaxial lip, from which the dorsal side of the carpel develops, is formed. The adaxial lip of the primordium develops more slowly and forms the "sill" of the carpel (McLean and Ivimey-Cook, 1956). This sill may enlarge and form the margins of the carpels (Fig. 163, nos. 1–7). It is assumed that the sill ori-

ginally consisted of the two basal laminar lobes which, as in the ontogeny of the peltate leaf, have fused. The area where the two margins fuse is termed the *cross-zone*. The ovule or ovules develop from this zone (Fig. 163, nos. 5, 6). In most cases the dorsal side of the carpel folds and closes over the sill. In a few genera of the monocotyledons, e.g. plants belonging to the Butomaceae, the primordia of the carpels are horseshoe-

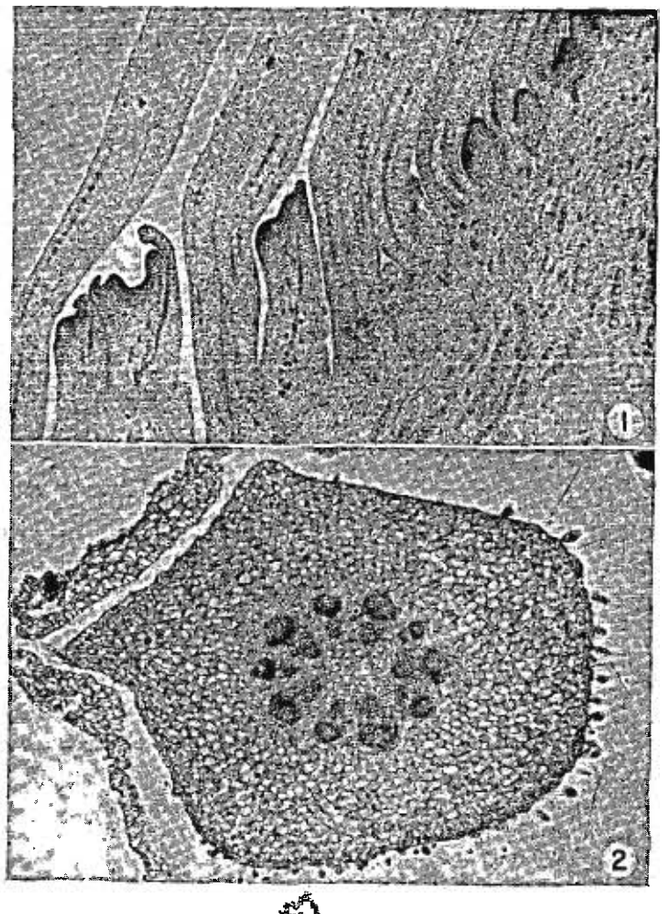


FIG. 165. 1, Portion of a longitudinal section of a developing inflorescence of *Musa* (Dwarf Cavendish banana) showing floral primordia in different stages of development. ×34. In the second primordium from the left, the depression that represents an early stage in the development of the inferior ovary, can be seen. 2, Cross-section of the pedicel of *Aquilegia caerulea* in which ten bundles, five large alternating with five small, can be distinguished. ×34.

shaped, in cross-section, and remain so almost until the maturation of the carpels, and so no sill is developed. In this case the fusion of the margins of the carpels is incomplete even in the mature carpel (Fig. 164, nos. 1–4).

In flowers with *syncarpous* gynoecia, i.e. those in which the carpels are fused, the ovaries may develop in two ways. In the first type, carpel primordia first appear separate and fuse later as a result of lateral growth. Subsequently, the carpels grow upwards as a unit on which the primordial apices are borne (Fig. 164, nos. 5–10). In the other type of development the carpels are already joined in the earliest stages of primordial development so that the ovary wall rises, from its initiation, as a ring. The regions of fusion between the carpels are distinguishable by inwardly directed folds (Fig. 162, nos. 5–7). During the very early stages of development of an inferior ovary, a depression can be distinguished in the centre of the developing flower (Fig. 165, no. 1). This depression gradually deepens. In the flower of *Musa*, three separate rounded carpel primordia can be distinguished before the formation of this depression.

Vascularization of the flower

The anatomical structure of the axis of the inflorescence and of the pedicel is similar to that of a typical stem; the vascular cylinder may be entire or split. Within the receptacle the shape of the stele becomes similar to that of the receptacle itself, i.e. the stele is usually widened at the base and narrows towards the upper part of the receptacle. From the stele of the receptacle the traces pass out to the various floral organs. The traces and the gaps split the stele into a characteristic network of vascular bundles (Fig. 168, no. 1; Fig. 170). The stele may be further split as a result of the reduction of vascular tissues, as occurs in a typical stem (Eames, 1931; Eames and MacDaniels, 1947; Tepfer, 1953). The traces of the various floral organs leave the stele in whorls or along a spiral line, in accordance with the arrangement of the organs on the receptacle. The traces of the uppermost carpels may, in certain plants, terminate the stele of the receptacle (Fig. 171, no. 1). In other plants, however, the stele continues above the level of the traces to the uppermost carpels. In this case the terminal bundles of the stele of the receptacle, which consist only of phloem or procambium, gradually fade out within the top of the receptacle (Fig. 171, no. 2).

The number of traces to the various floral organs varies. The number of traces to a sepal is usually equal to that supplying the foliage leaves of the same plant. Petals generally have one trace, but in some families three or more traces may be present. Stamens usually have a single trace but in some ranalian families and certain species of a few other families, e.g. the Lauraceae and Musaceae, three traces enter each stamen. Carpels may have one, three, five or more traces; three traces is the most common condition, but five also occur frequently. The median carpel trace leaves

the stele at a lower level than do the other traces. The continuation of this median trace constitutes the dorsal bundle of the carpel and the trace itself is termed the *dorsal trace*. The dorsal bundle is actually homologous to the leaf mid-rib. The two outermost traces on each side are termed the *marginal* or *ventral traces*, as the bundles that pass along the margins of the carpel develop from them. If the carpels are fused to form a syncarpous gynoecium these marginal bundles are found lateral to the dorsal bundle and if the carpels are folded inwards they are found ventrally

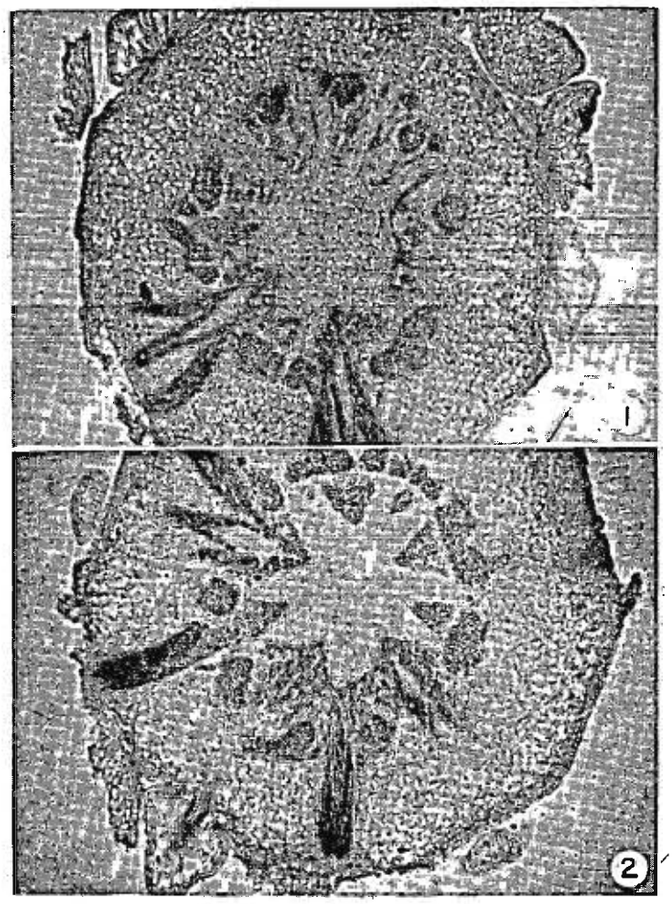


FIG. 166. Cross-section in the receptacle of *Aquilegia caerulea*. 1, At the level of the exit of the sepal traces, showing the traces to two sepals. Each sepal is supplied by three traces. ×36. 2, At a level a little higher than in no. 1 showing two single petal traces and the vascular supply, consisting of three traces, to one sepal. ×38.

relative to the dorsal bundle (Fig. 169, nos. 1, 2). As a result of the inward-folding of the carpel margins the ventral bundles are inverted—their phloem is directed towards the cavity of the ovary, and their xylem outwards. If more than three traces are present in a carpel the additional traces are present between the ventral and dorsal traces, and they are

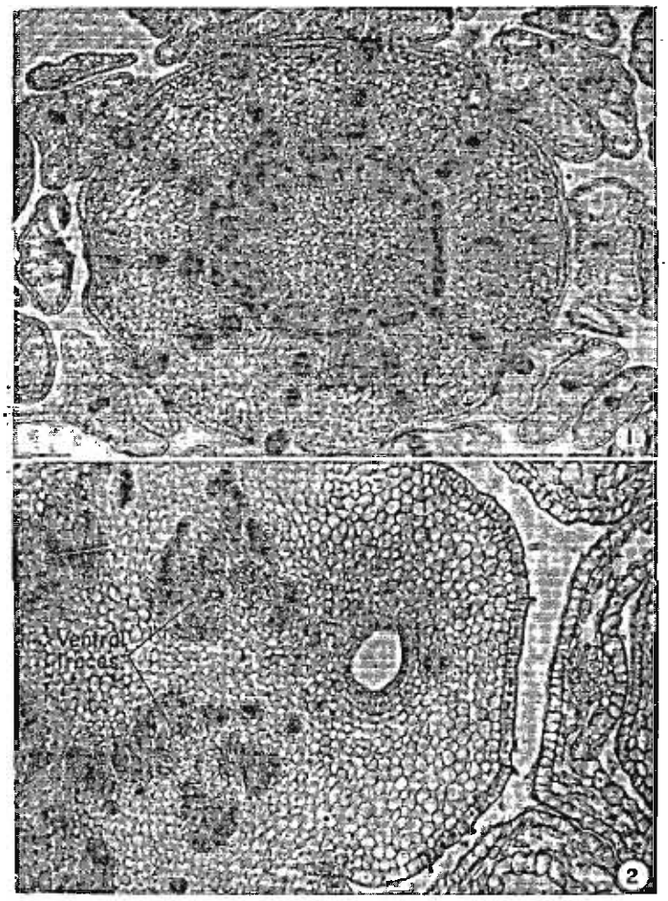


FIG. 167. *Aquilegia caerulea*. 1, Cross-section in the receptacle at the level of the exit of the traces to the numerous whorls of stamens. Within the receptacle the staminal traces are seen to be arranged in radial rows. ×35. 2, Cross-section in the basal portion of a single carpel in which the single dorsal trace and two ventral traces can be distinguished. In the ventral traces (but not in the branches of them that appear close to them in the micrograph) it can be seen that the xylem is directed outwards and the phloem inwards. ×110.

termed *lateral traces*. The vascular bundles of the carpels may branch and may even continue to do so during the development of the fruit.

The vascular bundles that supply the ovules usually originate from the ventral carpel bundles, or from branches of them that are present in the placenta (Fig. 169, no. 1). The ovular bundle is single and thin, and reaches the zone of the chalaza; it does not penetrate into the nucellus but in some genera branches of it enter into the integuments.

The structure of the receptacular stele and the system of vascular bundles within the floral organs is relatively complex even in the simpler types of flowers (i.e. those that are phylogenetically relatively primitive). The interpretation of floral vascularization becomes even more difficult in flowers in which fusion of the traces has taken place during the process of evolution. Eames (Eames, 1931; Eames and MacDaniels, 1947) gives *Aquilegia* of the Ranunculaceae and *Pyrola* of the Ericaceae as examples of flowers with simple vascular systems. In species of *Aquilegia* the pedicel contains five thick bundles which alternate with five thin bundles (Fig. 165, no. 2). These bundles fuse at the base of the flower to form an uninterrupted ring. Above this level five groups of sepal traces, each group consisting of three traces per single gap, depart from the stele (Fig. 166, no. 1). A little higher, alternating with the sepal traces, a single trace passes out to each of the five petals (Fig. 166, no. 2). Above the petal gaps the traces to the numerous stamens are found. Each stamen has a single trace (Fig. 167, no. 1). Above the uppermost whorl of stamens the stele once again becomes an uninterrupted ring. Shortly above this level five compound gaps of the carpels are formed. From the base of each such gap, the dorsal trace is given off and, from the sides, the pair of ventral traces (Fig. 170; Fig. 171, no. 2). The ventral traces invert immediately on their exit from the stele and so enter the carpel with the xylem directed outwards (Fig. 167, no. 2). Above this level the stele consists of five bundles which mainly consist of phloem. This vascular tissue gradually fades towards the rounded tip of the receptacle.

The type of vascular system that is exemplified by *Pyrola* (Fig. 171, no. 1) differs principally from the type of *Aquilegia* in the following features: (a) each sepal has only one trace; (b) above that level at which the dorsal carpel traces depart from the stele the remaining stelar bundles fuse in pairs to form five strands, each of which represents the two ventral traces; (c) no vestigial vascular tissue is found at the top of the receptacle.

VARIATIONS IN THE VASCULARIZATION OF THE FLOWER

During phylogenetic development of the flower, processes of cohesion, adnation and organ abortion have taken place. It is commonly accepted that during the process of evolution the external fusion of organs precedes

that of the inner tissues, and that the fusion of the vascular tissue represents the last stage in this process. Fusion of vascular bundles involves those bundles that were close to one another. The fusion may involve the traces alone or may include part of the bundles within the organs, and not very often does it continue throughout the entire length of the bundles. Usually there is ontogenetic and histological evidence that fusion has taken place. Evidence of aborted organs is assumed from the presence of rudimentary organs and persisting traces as compared with related flowers.

Bundle fusion

As a result of the cohesion of organs, in many cases the lateral and marginal vascular bundles and traces fuse. In the calyces of plants of the Labiatae different stages of vein fusion can be found. Thus, according to Eames (1931), in *Nepeta* and *Monarda* it is possible to discern that each sepal has a main vein and two lateral veins (Fig. 172, nos. 1, 3); in the calyces of *Ajuga* and *Physostegia* the neighbouring lateral veins are seen to be fused almost up to the base of the sinuses between the calyx lobes (Fig. 172, nos. 2, 4); in *Salvia* (Fig. 172, no. 5) two pairs of lateral veins are fused while the others remain free.

In sympetalous corollas vein fusion may also be found (Fig. 172, nos. 6–10). In the sympetalous flowers of the Rubiaceae, for example, it is still possible to discern fifteen veins, three in each petal. In the Compositae it is possible to find evidence of the fusion of the lateral bundles and of the loss of the median bundles (Koch, 1930).

In the gynoecium the fusion of the bundles takes place in the following ways. If the carpels are free the two ventral bundles approach one another on the ventral side of the primitive type of carpel that develops into a follicle (Fig. 169, no. 1). The ventral bundles may fuse from the base and the fusion may continue along the entire length of the carpel or along only part of it (Fig. 169, nos. 2, 3). A carpel with a single dorsal and a single ventral bundle may have two or three traces. In the former case one trace is related to the dorsal bundle and one to the ventral. In very reduced carpels, as, for instance, those in cypselae, there is sometimes only one trace, and it splits at the base of the locule of the carpel. In such a trace the three original traces are fused. If the carpels are fused, two types of fusion are distinguished. On the one hand, when a large portion of the carpel is folded inwards and the placenta is axile, the ventral bundles are brought to the centre of the ovary where a pair of inverted ventral bundles of a single carpel or those of two adjacent carpels fuse (Fig. 172, nos. 16–18). The lateral bundles (i.e. those between the dorsal and ventral bundles) of two neighbouring carpels may also fuse in such an ovary

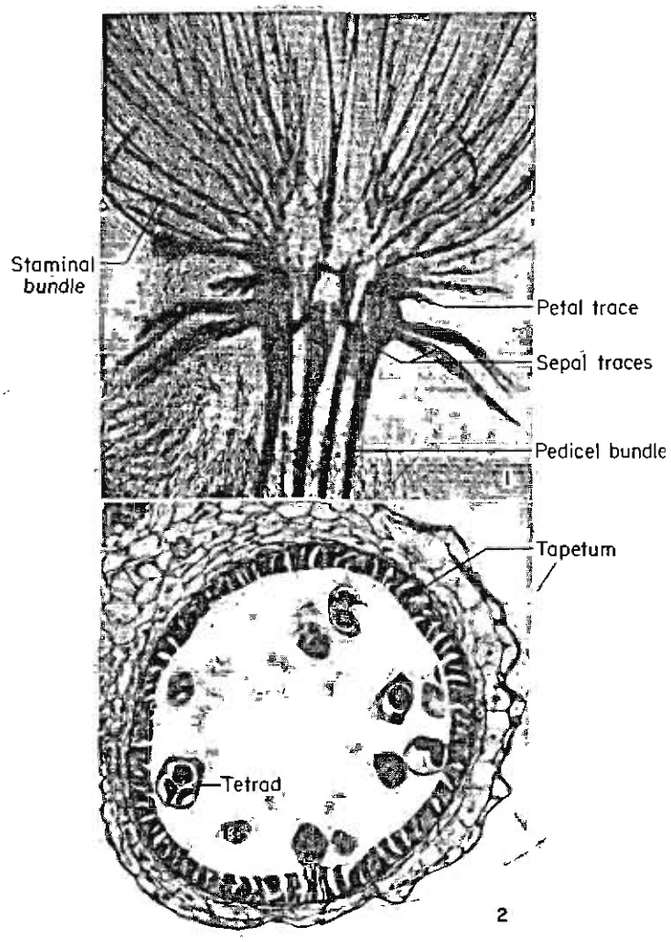


FIG. 168. 1, Photograph of a cleared flower of *Aquilegia caerulea* as seen in lateral view; the sepals and petals have been removed. ×20. 2, Micrograph of a cross-section of a young pollen sac of *Passiflora caerulea* showing a glandular tapetum. ×130.

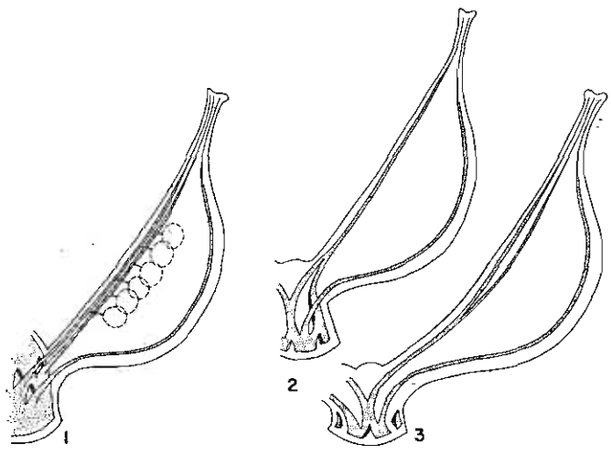


FIG. 169. Diagrams illustrating the carpellary vascular supply. 1, A carpel supplied by three traces each of which is accompanied by a separate gap; bundles remain unfused within the carpel to the stigma. 2, A carpel in which the two ventral traces are fused from the base of the carpel. 3, A carpel in which the ventral traces arise fused, but in which they separate in the basal portion of the carpel. (Adapted from Eames and MacDaniels, 1947.)

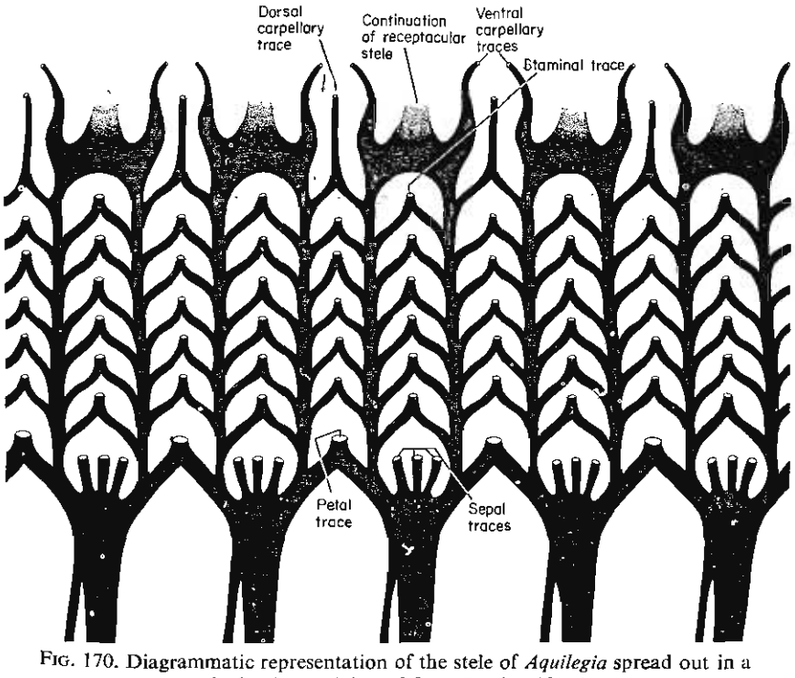


FIG. 170. Diagrammatic representation of the stele of *Aquilegia* spread out in a single plane. (Adapted from Tepfer, 1953.)

(Fig. 172, nos. 16–18). On the other hand, if the carpels become fused while they are still open and so form a single common locule with parietal placentation, the ventral bundles are not inverted and they occur in pairs along those lines where the cohesion of the carpel margins takes place, or they may fuse to form common bundles (Fig. 172, no. 11).

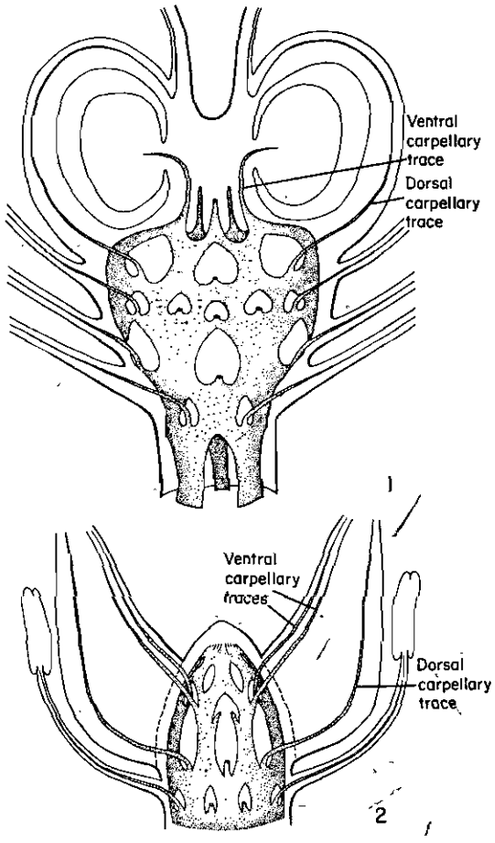
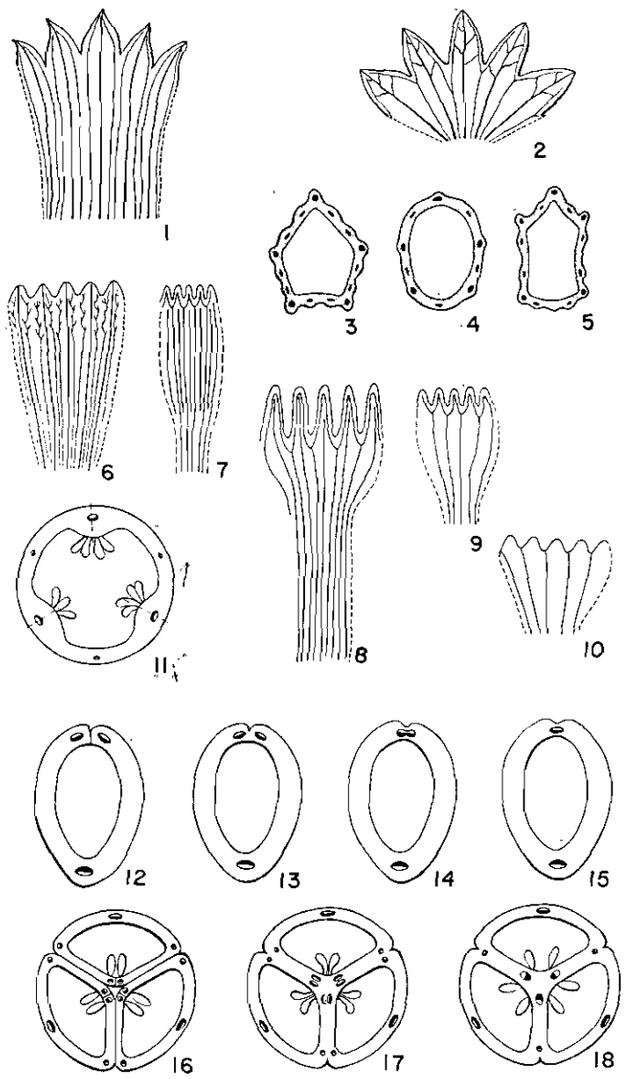


FIG. 171. Diagrammatic representation of different types of floral vascularization. 1, *Pyrola*, showing an entire flower. 2, *Aquilegia*, showing the upper part of a flower. Vascular tissue stippled. (Adapted from Eames and MacDaniels, 1947.)

In addition to the fusion of bundles as a result of cohesion of organs, bundle fusion also results from adnation, i.e. the fusion of organs of different whorls. Bundles that are radially or tangentially close to one another may fuse, and this process may involve different numbers of bundles which may belong to two or more whorls. Different stages in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the fusion of the staminal bundles with those of the petals (epipetalous stamens) may be seen, for example, in the Crassulaceae (Fig. 173, no. 7). In flowers of plants belonging to the Rosaceae (Fig. 173, nos. 3–6), it is possible to discern the fusion of bundles from more than two whorls (Jackson, 1934).

The inferior ovary

The problem of the phylogenetic development of the inferior ovary still challenges flower morphologists. The problem is whether the gynoecium has sunk into a concave receptacle which then surrounded the carpels and fused with them (axial theory), or whether the inferior ovary arose as a result of the cohesion and adnation of the lower portions of all the floral organs to the gynoecium, which they surround (appendicular theory). In order to solve this problem different methods within the field of comparative morphology, involving ontogeny, histology, teratology and palaeontology have been used. Much attention has been paid to the floral vascular anatomy (Douglas, 1944). The latter line of investigation in connection with the inferior ovary has revealed the following features. In the wall of the inferior ovary of certain plants, e.g. *Hedera* (Fig. 173, no. 1), separate traces which are related to the different floral organs are found. In many plants, e.g. *Juglans* (Fig. 173, no. 2) and a few species of the Ericaceae, different stages of bundle fusion have been observed in the

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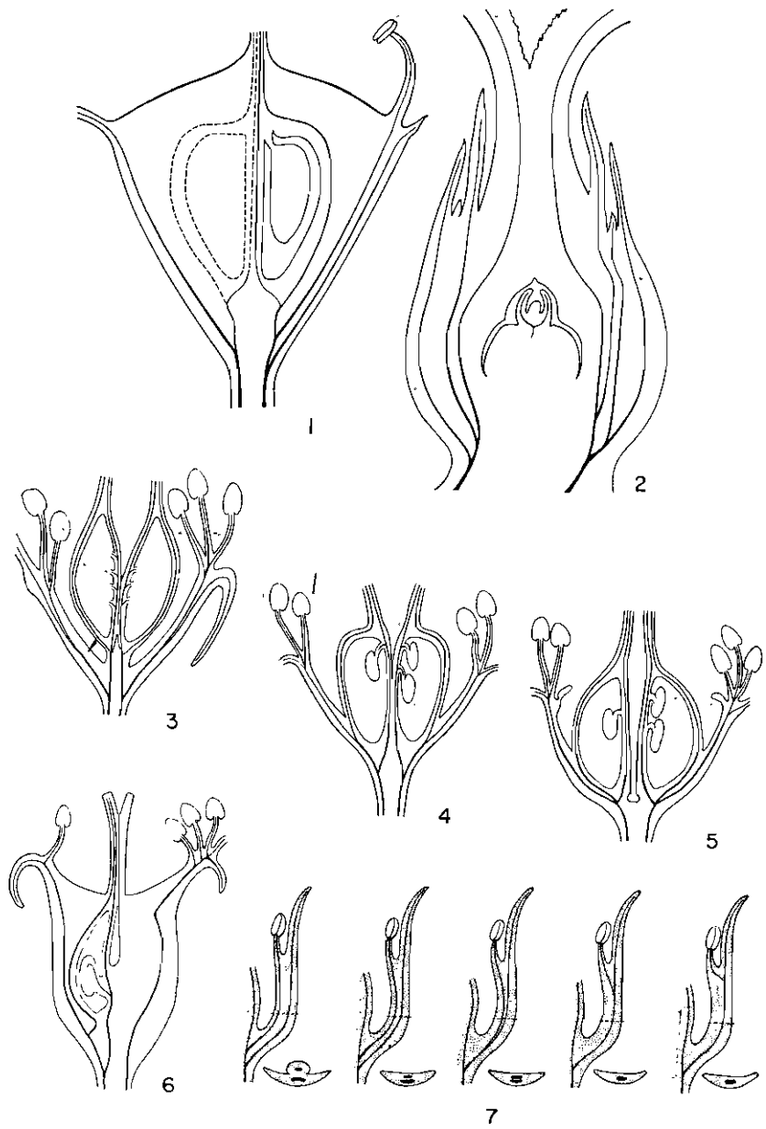
FIG. 172. 1–5, Stages in the fusion of lateral bundles in gamosepalous calyces. 1, Calyx of *Nepeta veronica* cut and spread out; the lateral bundles are unfused. 2, Calyx of *Ajuga reptans* in which the lateral bundles are fused. 3, Diagram of the cross-section of the calyx of *Monarda didyma* in which the lateral bundles are free. 4, Cross-section of the calyx of *Physostegia virginiana* in which the lateral bundles are fused. 5, Cross-section of the calyx of *Salvia patens* in which two pairs of lateral traces are fused. 6–10, Stages in the fusion of lateral bundles in gamopetalous corollas. 6, *Hamelia patens*, in which the lateral traces are unfused. 7, *Senecio fremontii*. 8, *Anastrophia ilicifolia*. 9, *Chrysanthemum leucanthemum*. 10, *Xanthium orientale*. 11–18, Diagrams of cross-sections of carpels showing different stages of cohesion. 11, *Reseda odorata* in which the placentation is parietal. 12–15, Different stages in the fusion of the ventral bundles in follicles. 16–18, Different stages in the phylogenetic development of the syncarpous ovary from the stage where the tissues and vascular bundles of each carpel are unfused through the stage where the carpellary tissues but not the vascular tissues are fused to the final stage where the carpellary tissues and lateral and ventral bundles are fused. In nos. 11–18 the xylem is represented by solid black and the phloem is white. (Nos. 1–5 and 11–18, adapted from Eames and MacDaniels, 1947; nos. 6–10, adapted from Koch, 1930.)



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wall of the inferior ovary (Manning, 1940; Douglas, 1944; Eames and MacDaniels, 1947; Eames, 1961). In relation to these plants, therefore, it is possible to conclude from the vascular anatomy that the wall of the inferior ovary consists of the ovary wall proper together with the other floral organs that are fused with it.

In species belonging to the Cactaceae and Santalaceae (Fig. 174, no. 1), inverted vascular bundles, i.e. those with inwardly directed phloem and outwardly directed xylem, can be found along the entire length of the inferior ovary wall (Smith and Smith, 1942; Tiagi, 1955). This feature suggests that in these species the inferior ovary has developed as a result of the involution of the receptacle, as the sinking of the gynoecium into the receptacle necessitates an inward folding of the upper portion of the receptacular stele. In *Rosa*, Jackson (1934) found, according to the vascular anatomy, that the lower portion of the fleshy fruit consists of receptacular tissue, while the upper portion of it consists of fused floral organs (Fig. 174, nos. 2–4). Jackson also showed that various intermediate stages, which demonstrate the evolution of the rose fruit, can be seen in related genera. The fruit of *Pyrus malus* var. *paradisiaca* and related genera apparently consists mainly of true ovary wall and of other floral organs that are fused to it, and the receptacle constitutes a very small portion, which is not easily discernible, at the base of the fruit (Fig. 211, no. 6) (MacDaniels, 1940). The adnation of the bundles in an inferior ovary that is developed from the fusion of the ovary wall proper to other floral organs is not equal in different radii, neither in the number of traces involved nor to the extent to which they are fused.

FIG. 173. 1, Diagram of a longitudinal section through the inferior ovary of *Hedera helix* in which there is no fusion between the sepal, petal and staminal bundles, or between these bundles and the carpellary bundles. 2, Longitudinal section of the flower, including bracts, of *Juglans nigra* showing the fusion, in their basal portions, of the bundles of the different organs. 3–6, Longitudinal sections of flowers of related genera of the Rosaceae showing different degrees of adnation of the hypanthium to the carpels. 3, *Physocarpus opulifolius* in which the ovary is superior and the sepals, petals and stamens are fused, but not to the carpels. 4, *Sorbus sorbifolia* in which the hypanthium is adnated to the base of the carpels. 5, *Spiraea vanhouttei* in which the hypanthium is adnated to the carpels to a level half way along the ovary. 6, *Pyrus malus* var. *paradisiaca* in which the hypanthium is adnated to the ovary throughout its length. 7, Diagrams showing different degrees of vascular fusion during the adnation of a stamen and petal, as seen in both longitudinal and cross-sections. (Nos. 1, 6 and 7, adapted from Eames and MacDaniels, 1947; no. 2, adapted from Manning, 1940; nos. 3–5, adapted from Jackson, 1934.)

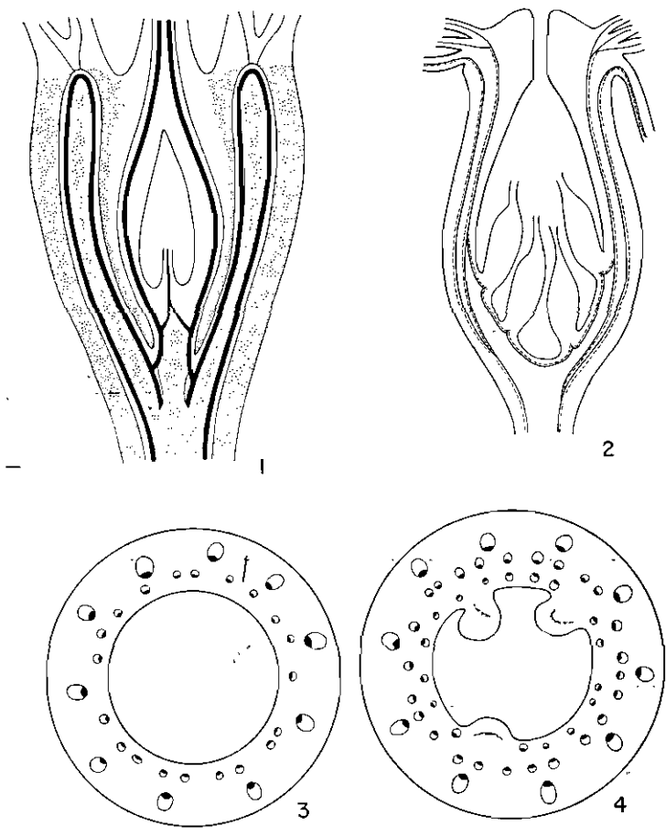


FIG. 174. 1, Diagram of a longitudinal section of the inferior ovary of *Darbya* (Santalaceae) showing the vascularization; xylem—black and phloem—white. 2–4, *Rosa helenae*. 2, Diagram of a longitudinal section of the flower; broken line, phloem and solid line, xylem. 4, Diagram of a cross-section in the lower quarter of the hypanthium showing the vascular bundles (xylem—black, phloem—white). The arrangement of the vascular tissues in the innermost row is seen to be inverted, a fact which is evidence of invagination at this level. 3, A cross-section at a level higher than in no. 4 in which there is no inversion of the vascular tissues indicating that at this level there is no invagination. (No. 1, adapted from Douglas, 1944; nos. 2–4, adapted from Jackson, 1934.)

In addition to the fusion of the floral organs of a single flower among themselves, fusion may occur between flowers and the bracts accompanying them, e.g. *Lonicera* and *Juglans*, and even between several flowers, e.g. in certain species of *Lonicera*, *Cornus* and *Maclura*. These features are also often accompanied by the fusion of bundles (Manning, 1940; Eames and MacDaniels, 1947).

Vestigial vascular bundles

The presence of vestigial vascular bundles, in certain positions, is frequently taken as proof of the degeneration of the organs that were originally present in the same position in the ancestral floral type. Vestigial petal traces may be found in the receptacle of apetalous flowers, e.g. *Aristolochia*, species of *Rhamnus*, *Salix* and certain species of *Quercus*. Vestigial staminal traces can be found in the Scrophulariaceae, Labiatae, Cucurbitaceae, and in certain genera of other families. In the Caprifoliaceae, Ericaceae, Rutaceae and Valerianaceae vestigial carpel traces are found. Such vestigial traces may also be found in unisexual flowers. Degenerate ovules are commonly associated with vestigial bundles.

The reduction that has taken place during the evolutionary specialization of the floral organs is often accompanied by the reduction of the vascular supply to the organs. This is exemplified by the development of the achenium or cypsela, which contains a single ovule, from a legume or follicle, which contains several ovules, and by the reduction of the corolla in the capitulum of the Compositae. Such reduction is recognizable by the shortening of the bundles.

In some carpels, in which much reduction has taken place, only one bundle, which enters the ovule directly from the receptacular stele, is found. In stamens the bundles may sometimes terminate at the base of the filaments instead of reaching the anther. In the sympetalous corollas of many of the Compositae the median bundle is lost and lateral bundles may also become reduced, and they even disappear in the corollas of certain plants (Chute, 1930; Eames, 1931).

The importance of the structure of the floral vascular system in the interpretation of the morphological structure and the clarification of the phylogenetic relationships between different plants is still debatable (Henslow, 1891; Sporne, 1958). Puri (1951), who reviewed the relevant literature on floral anatomy, came to the conclusion that this method of research has contributed much to the better understanding of the angiosperm flower. However, he stresses the necessity of regarding the structure of the vascular system of the flower as only one important aspect of the problem of floral morphology. According to Puri the study of the external structure of organs and their ontogenetic development should not be neglected.

In spite of the above-mentioned reservations, the vascularization of the flower represents an additional feature which enriches our ability to tackle evolutionary and taxonomic problems.

Histology of sepals and petals

The external structure of sepals and petals may be leaf-like. However, the internal structure only of green sepals resembles that of foliage leaves and the internal structure of coloured sepals and petals is distinctly different.

In the perianth the vascular system is usually only poorly developed and the veins usually lack sclerenchyma. The mesophyll commonly consists of spongy parenchyma only and its cells contain chromoplasts or pigments in the cell sap or both. Usually the epidermal cell walls are thin. The anticlinal walls of these cells are, in many flowers, folded or undulated and they are arranged so that the projections of the cells dove-tail one into the other, a feature that strengthens the epidermis. At the base of the petals, as well as along the length of the veins, the anticlinal walls are usually straight even when they are wavy in the other epidermal cells. The outer walls of the epidermal cells commonly have papillae, which make the petals glisten. More papillae are present on the adaxial than the abaxial epidermis and they are not developed at the base of the petals. Stomata, if present, are scanty and non-functioning. Trichomes may sometimes be present on sepals and petals. Sometimes intercellular spaces, covered by cuticle (Hiller, 1884), are formed in the epidermis of petals. The thickness of the cuticle varies in different plants and it may be variously sculptured (Martens, 1934) (Fig. 58, no. 2). Various pigments are found in the epidermal cells of the petals and sepals. The less specialized the petals are, the more their internal structure resembles that of foliage leaves, that is, the veins and the mesophyll are better developed, a palisade-like tissue is present, the epidermis is devoid of papillae and there are many stomata.

The stamen

PHYLOGENY

The stamens and carpels of highly specialized flowers differ greatly in structure and general shape from foliage leaves. Different opinions still exist as to the morphological interpretation and evolutionary development of the stamens and carpels (Parkin, 1951). The most commonly accepted theory is that these organs are homologous to leaves. The opinion also exists that the development of the stamen can be explained on the basis of

the telome theory, that is, from primitive dichotomously branched axes. According to this theory the stamen has developed as the result of the reduction and fusion of a system of axes that bore sporangia at their tips (Wilson 1937, 1942). New light was thrown on the phylogeny of stamens and carpels by Bailey and his co-workers from their morphological and comparative anatomical research in many families of the Ranales. From these investigations it has become apparent that in the woody species of the Ranales that exist today not only primitive stages of xylem development have been preserved, but also primitive types of stamens and carpels (Bailey and Smith, 1942; Bailey and Nast, 1943a, b; Bailey, Nast and Smith, 1943; Bailey and Swamy, 1949, 1951; Canright, 1952; Bailey, 1956). A very primitive type of stamen is found in the genus *Degeneria;* here no filament, anther or connective can be distinguished as the stamen is broad and leaf-like, and has three vascular bundles. The four pollen sacs (the microsporangia) are deeply sunk into the abaxial side of the stamen (Fig. 176, nos. 1, 2). The pollen sacs are found between the lateral and median bundles. Similar stamens are found in other ranalian genera, e.g. *Austrobaileya, Himantandra* and certain genera of the Magnoliaceae. In the Magnoliaceae intermediate stages may be found from broad stamens with three bundles and laminal pollen sacs, i.e. pollen sacs distant from the margins, as in *Degeneria,* to stamens with marginal pollen sacs and distinct filaments and anthers (Canright, 1952).

STRUCTURE AND TISSUE DIFFERENTIATION

The epidermis of the filament possesses a cuticle and in certain species, trichomes. The filament consists of parenchyma with well developed vacuoles and small intercellular spaces. Often pigments are present in the cell sap. The size and external shape of angiosperm stamens varies greatly, but the anther generally contains four pollen sacs (microsporangia) which are paired in two lobes. The two lobes are separated by a zone of sterile tissue which is termed the *connective.* A vascular bundle passes through the connective (Fig. 175, nos. 1–3). According to Boke (1949), who worked on *Vinca rosea,* even some time after the region of the developing anther becomes discernible in the staminal primordium, the anther still consists only of protoderm and a mass of ground meristem. All of the subepidermal layer of the young anther may be sporogenous, but actually the sporogenous tissue is developed from four cell regions which are located in the four angles of the developing anther. In each of these regions there is a row of hypodermal initials which divide periclinally to form two layers (Fig. 176, nos. 4–8). The inner layer of these initials constitutes the *primary sporogenous cells,* which by further division form the *pollen mother cells.* The outer layer of the above initials constitute the *primary parietal cells,*

from which the wall of the pollen sacs and a large portion of the *tapetum* develop, as a result of periclinal and anticlinal cell division. The tapetum apparently serves for the nourishment of the developing pollen mother

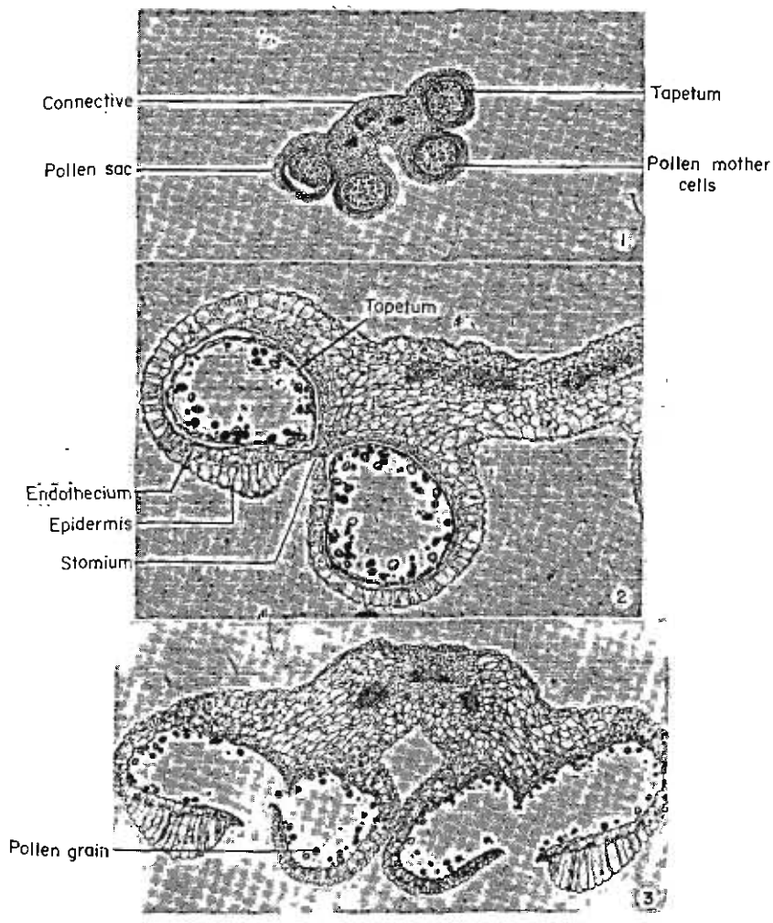


FIG. 175. Micrographs of cross-sections of the anthers of *Passiflora caerulea* at different stages of development. 3, Mature anther after dehiscence. 1 and 2, ×30; 3, ×26.

cells and microspores (pollen grains). The outermost layer of parietal cells is located immediately below the epidermis of the anther. Prior to the liberation of the pollen grains several wall thickenings develop in each of the cells of this layer. However, no thickening is developed in the outer

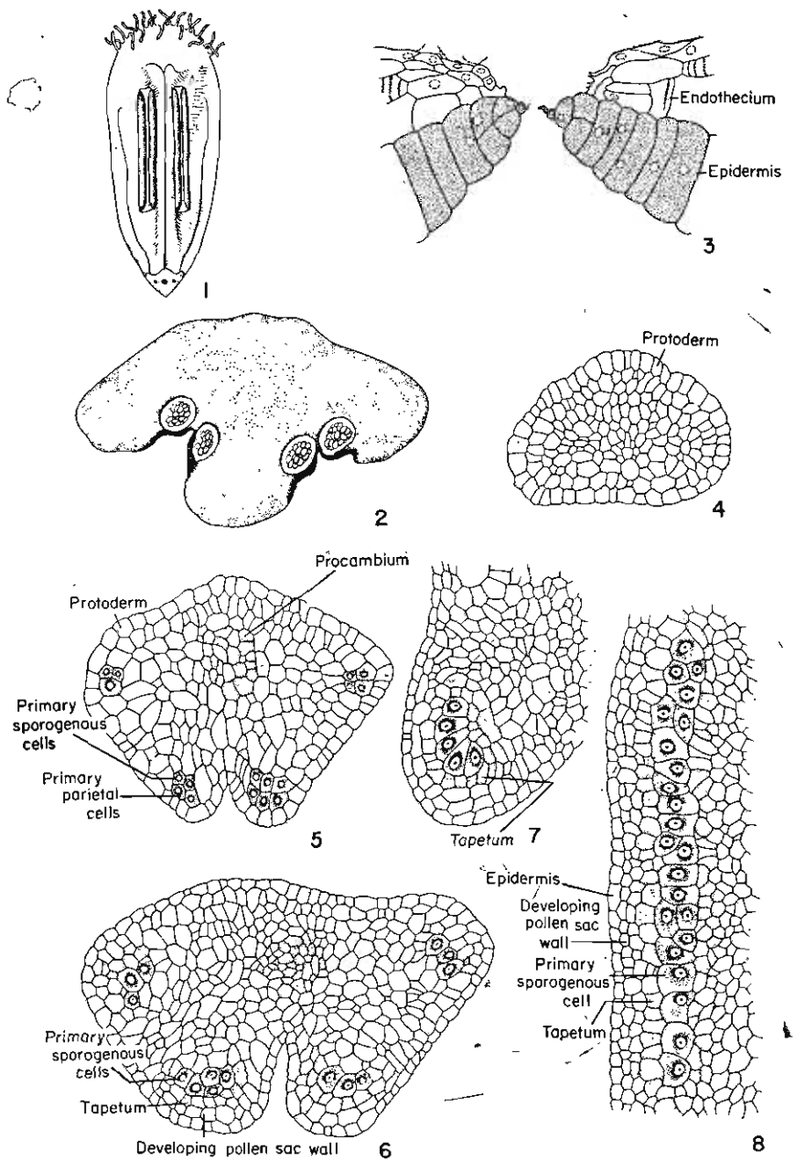


FIG. 176. 1 and 2, Stamen of *Degeneria vitiensis*. 1, Drawing of an entire stamen, showing a pair of sporangia between each of the lateral and median veins. 2, Diagram of a cross-section of the stamen showing the four deeply embedded sporangia and endothecium (shaded black). 3, Portion of a cross-section of the anther of *Lilium* showing the structure of the stomium. 4–8, Development of the pollen sacs of *Vinca rosea*. 4–7, In cross-section. 8, In longitudinal section. (Nos. 1 and 2, adapted from Bailey and Smith, 1942; no. 3, adapted from Esau, 1953; nos. 4–8, adapted from Bakr, 1949.)

wall closest to the epidermis. Each thickening is U-shaped with the gap directed towards the epidermis (Fig. 175, no. 2). This cell layer is usually termed the *endothecium* and the opening of the pollen sacs is brought about by this layer. The opening mechanism is described as follows. During the dehydration of the anther the endothecium loses water. As the water content of these cells decreases the walls of each cell are drawn toward its centre as a result of the cohesion forces between the water molecules and the adhesion forces between the water and the cell walls. Because of the

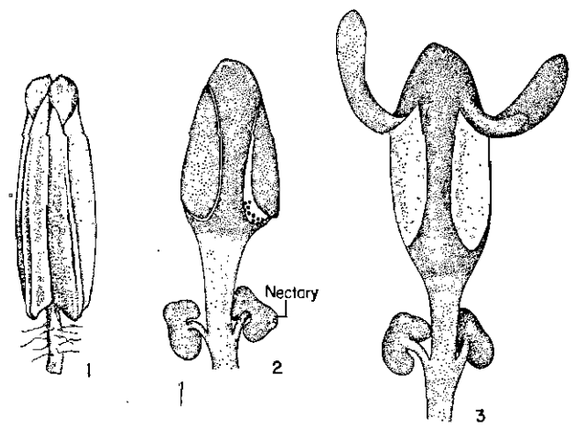


FIG. 177. Types of anther dehiscence differing from the ordinary. 1, Anther of *Solanum villosum* showing the apical pores. 2 and 3, Anther of *Laurus nobilis* showing different stages in dehiscence by lateral valves.

absence of thickenings in the outer periclinal wall, it becomes more folded than the anticlinal and the inner periclinal walls which have thickenings; thus, as a result of water loss, the cell appears trapezium-shaped in cross-section. As all the endothecial cells lose water almost at the same time and all the external walls fold and wrinkle, the endothecium shrinks in a manner that results in the opening of the anther. The cells in the region along which anthers dehisc are thin-walled. In most plants the regions of dehiscence are in the form of longitudinal slits between the two pollen sacs of each lobe. Each such slit is termed a *stomium*. Prior to dehiscence part of the partition between the two sacs of a lobe usually disintegrates. After this the region of dehiscence is covered only by the epidermis. The epidermal cells, in this region, are extremely small, especially in comparison with the neighbouring epidermal cells, and they are easily ruptured when the anther ripens (Fig. 175; Fig. 176, no. 3). Another type of stomium, common in the Ericaceae and in *Solanum*, is that occurring at the top of the

anther only (Fig. 177, no. 1). Openings may also develop on the sides of the anther as, for example, in the Lauraceae (Fig. 177, nos. 2, 3).

The cell layer or layers below the endothecium both stretch and become compressed during the development of the pollen-sac and in many plants they are obliterated so that it is difficult to distinguish them in mature anthers immediately prior to dehiscence (Fig. 175, no. 2).

The formation of the tapetum takes place as a result of gradual differentiation in the anther wall. In those cases where additional tapetal layers

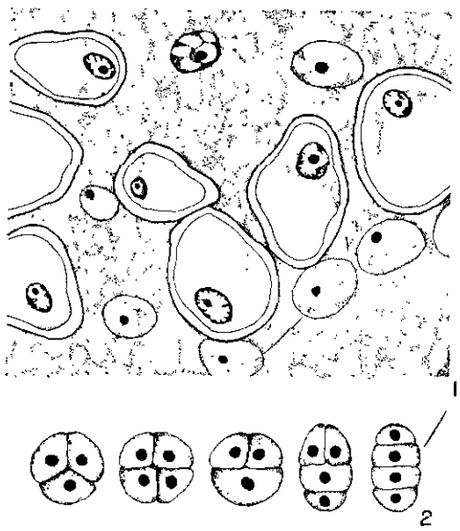


FIG. 178. 1, Diagram of portion of a cross-section of the pollen sac of *Symphoricarpus racemosus* showing an amoeboid tapetum. 2, Different types of arrangement of the pollen grains in the tetrad. From left to right—tetrahedral, isobilateral, decussate, T-shaped, linear. (Adapted from Maheshwari, 1950.)

develop, they arise from cell division in other cells of the anther, and especially of those on the inner side of the sporogenous tissue (Fig. 176, nos. 7, 8). In some cases the sporogenous tissue itself may take part in tapetum formation (Eames, 1961). The tapetal cells are distinctly enlarged, rich in protoplasm and they may be multinucleate or polyploid. Various irregular mitotic divisions and nuclear fusion take place in these cells (Maheshwari, 1950). Two types of tapetum are distinguished—*glandular* or *secretory tapetum* (Fig. 168, no. 2) in which the cells remain in their original position where they later disintegrate and their contents are absorbed by the pollen mother cells and the developing pollen grains; and *amoeboid tapetum* (Fig. 178, no. 1) in which the protoplasts of the tapetal cells penetrate between the pollen mother cells and the developing pollen grains where they fuse among themselves to form a *tapetal periplasmodium*.

POLLEN GRAIN DEVELOPMENT

The primary sporogenous cells commence to divide mitotically, in different planes, together with the development of the pollen sac wall. The derivatives of these divisions are the *pollen mother cells*, which are also known as *microsporocytes*. Each mother cell undergoes a meiotic division to form a *tetrad* of pollen grains, i.e. four haploid microspores. Shortly before the meiotic division, the pollen mother cells usually separate one from the other, their protoplasts round off and they become covered by a thick gelatinous wall which stains with callose stains. The arrangement of the pollen grains in the tetrad differs in different species and sometimes it may even differ in the same species (Fig. 178, no. 2). Apparently the two most common arrangements are the tetrahedral and the isobilateral ones.

On the basis of the manner of the wall formation accompanying the meiotic division of the pollen mother cell, two types are distinguished: (1) the *successive type* in which each of the nuclear divisions is accompanied by wall formation (Fig. 179, nos. 1–5); (2) the *simultaneous type* in which peripheral constrictions commence to develop only after the four nuclei have been formed, and the wall formation precedes from these constrictions inwards (Fig. 179, nos. 6–9). The simultaneous type is more typical of dicotyledons, while the successive type is typical of many monocotyledons, but this systematic division is not absolute and many exceptions exist. Also there is no correlation between these types of wall formation and the arrangement of the grains in the tetrad.

In most cases the pollen grains of each tetrad separate from one another and they lie freely in the pollen sac. In some plants, e.g. the Ericaceae, the pollen grains remain in tetrads even when mature (Fig. 181, no. 4). In certain plants, e.g. *Acacia*, the tetrads are stuck together in groups, which may contain as many as 64 pollen grains (Fig. 182, no. 1); these groups are found in separate chambers formed by the development of transverse partitions in the pollen sacs. In some plants, e.g. the Asclepiadaceae, all the pollen grains of a sac are united in a single compact mass; such a mass is termed a *pollinium* (Fig. 179, no. 10). In Orchidaccae pollinia are also formed, but in certain genera of this family the pollinium is less compact as it comprises smaller groups of pollen grains, i.e. *massulae*, which are loosely joined among themselves, usually by means of viscin threads (Fig. 179, no. 11).

The first-formed wall that separates each of the pollen grains consists of callose and pectic substances, that is, the same material as the general wall of the tetrad, and it is termed the *special wall.*

A young pollen grain has a large central vacuole, but with maturation the nucleus enlarges and the cytoplasm becomes denser and increases in amount, so that when the grain is mature the cytoplasm obliterates the vacuole. Mature pollen grains contain large amounts of starch or, in cer-

tain species, fatty substances which are apparently absorbed from the tapetum. In many plants the starch disappears from the pollen grains during the ripening of the anther, while in others the starch disintegrates only in the pollen tube. It is assumed that there is a connection between the disintegration of the starch and the high osmotic pressure of the pollen

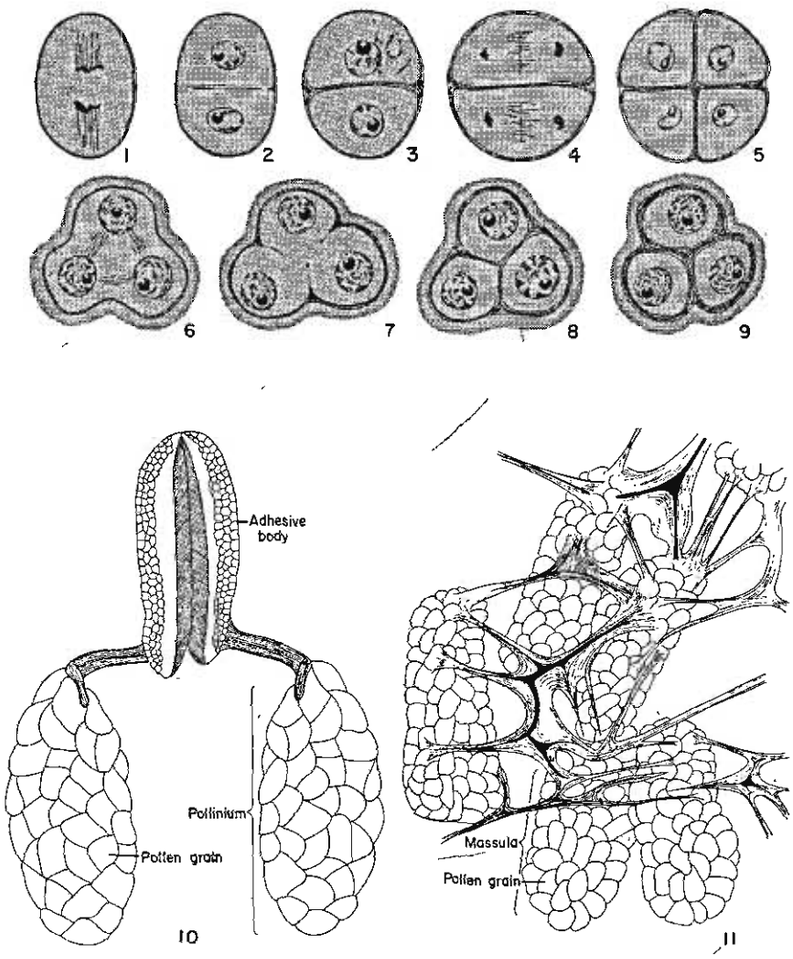


FIG. 179. 1–9, Different types of wall formation in pollen mother cells. 1–5, Successive type in *Zea*. 6–9, Simultaneous type in *Melilotus alba*. 10, Diagram of the paired pollinia of *Asclepias* which are joined by the adhesive body. 11, Diagram of a group of massulae from a pollinium of a plant belonging to the Orchidaceae showing the connecting viscin threads. (Nos. 1–9, adapted from Foster and Gifford, 1959; nos. 10 and 11, adapted from Schoenichen, 1922.)

tubes which is higher than that of the cells of the style through which the tube passes.

The chemical analysis of mature pollen grains shows the following composition (McLean and Ivimey-Cook, 1956):

proteins	7·0–26·0%	ash	0·9–5·4%
carbohydrates	24·0–48·0%	water	7·0–16·0%
fats	0·9–14·5%		

Mature pollen grains usually have two walls—the outer wall or *exine*, and the inner wall or *intine*. The intine participates in the formation of the pollen tube. The exine at first appears within the special wall as a thin membrane. With further development this membrane thickens discernibly, and two layers become distinguishable in it; the outer of these two layers is termed the *sexine* and the inner, the *nexine* (Erdtman, 1952). The sexine is thin and has a high refractive index and, therefore, it is not easily seen. The surface of the sexine is at first smooth but later, after the formation of the nexine, many types of projections may develop on it. In the *apertures*, regions of characteristic shape from which the pollen tubes emerge, the exine may be completely absent or it may be represented by the nexine only (Erdtman, 1952). The nexine is relatively thick and is impregnated with cutins. The specific cutin present in the exine has been termed *sporopollenin* (Frey-Wyssling, 1959). This substance is more stable than other cutins and suberin. It is also found in the walls of fungal spores. The preservation of pollen grains in peat and in older deposits is apparently due to the presence of sporopollenin.

The intine is not of constant thickness on the circumference of the pollen grain and it is always thicker at the apertures. The inner part of the intine apparently contains cellulose and the outer part, pectin. Callose apparently also occurs in the intine at the apertures. The intine readily absorbs water, as a result of which it swells greatly, especially at the apertures. Because of this, the nexine, if present in the apertures, is ruptured and the intine emerges.

With the development of the pollen grain walls, the mother cell walls and special walls are destroyed and dissolved. The substances of these walls mix with those of the tapetum, and the young grains thus become suspended in a colloidal liquid from which they absorb nutrients. According to Strasburger (1889) the entire exine is secreted from the protoplast of the pollen grain, while according to some workers (Mezzetti-Bambacioni, 1941) it is possible that the tapetum participates in the formation of the exine.

Numerous characteristic projections and sculpturings develop on the outer surface of the pollen grain. Only in a few plants, such as species of the Gramineae, are the pollen grains smooth. In most cases the sexine constitutes a layer of drumstick-shaped rods, which are termed *pila*. In

many plants the heads of these rods fuse to form the *tegillum* (a roof-like layer) which may also be formed by a membrane covering the heads of the rods. The tegillum is generally perforated by minute pores, and spines, warts or other structures may develop externally on it. The formation of air sacs is brought about by the separation of the pila from the

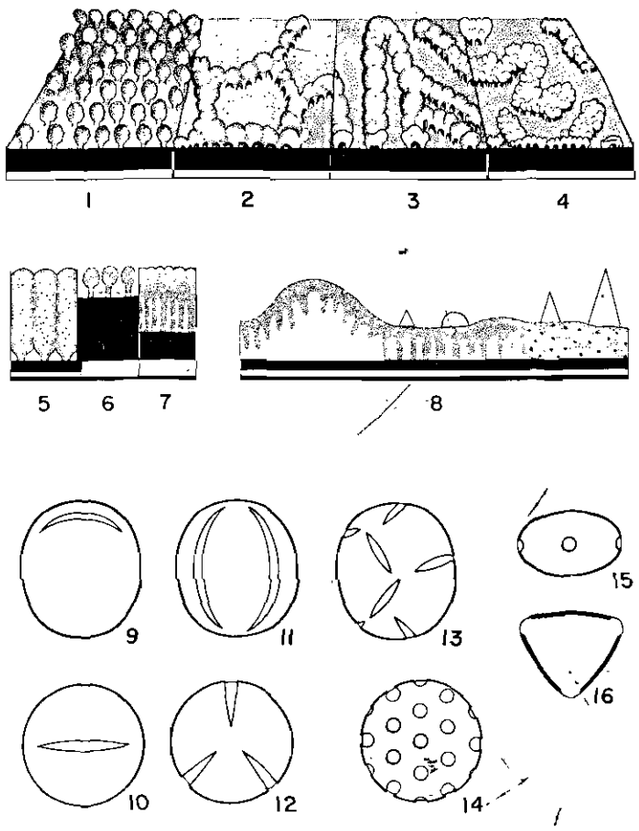


FIG. 180. 1–8, Sculpturing on pollen grains. 1, Scattered pila. 2–4, Adherent pila arranged in characteristic reticulate patterns or in rows. 5, Cross-section of a pollen-grain wall with a thick sexine. 6, As in no. 5, but with thin sexine. 7, Cross-section of pollen-grain wall on which the heads of the pila are fused to form a tegillum. 8, Different types of pila fusion, and the resulting types of structure. On the left, disappearance of the pila bases; on the right, development of spines, etc. 9–16, Arrangement and types of apertures. 9 and 10, Unisulcate pollen grain. 9, Lateral view. 10, Polar view. 11 and 12, Tricolpate pollen grain. 11, Lateral view. 12, Polar view. 13, Rugate pollen grain. 14, Porate pollen grain. 15 and 16, Pollen grain with three pores. 15, Lateral view. 16, Polar view. (Nos. 1–8, adapted from Erdtman, 1952.)

nexine. The reticulate, striped or other patterns of sculpturing, which are visible on the surface of many pollen grains, result from the particular arrangement of the pila (Fig. 180, nos. 1–8). In many plants there is a fatty substance on the exine which, apart from the spines and other appendages of the grain wall, aids the adhesion of the pollen to pollinating insects.

In addition to the different sculpturings on the surface of pollen grains, which result from the structure of the sexine, there are also many other morphological characteristics that are used in classification of the pollen (Fig. 181, nos. 1–4; Fig. 182, nos. 1–4). From pollen analysis it is possible to determine the species of plants occurring in a certain area as well as the existence of plant species, of which no other relic has been preserved, in early geological times. Quantitative pollen analysis made on recent geological layers has greatly helped in the understanding of the history of floras in many parts of the world. Because pollen grains are one of the most important causes of allergic diseases, and especially of those of the respiratory tract, much attention has been paid to the analysis of pollen present in the atmosphere in the different seasons. Much importance is also attached to the determination of the pollen collected by bees in research on honey plants. As a result of this wide range of research, based on the variability of pollen grains, a very detailed nomenclature of the structural characteristics of pollen has been developed which enables exact morphological descriptions to be made of different pollen grains (Wodehouse, 1935; Erdtman, 1952).

Oval pollen grains are commoner among monocotyledons than among dicotyledons, but this is not a feature distinguishing between these two groups. In the monocotyledons the pollen grains of a single tetrad are usually arranged in one plane, while in dicotyledons the arrangement is usually tetrahedral. Pollen grains that are arranged in one plane are somewhat boat-shaped, and are bilaterally symmetrical. Monocotyledonous pollen grains usually have one aperture, and those of dicotyledons usually have three which develop in those regions where the grains are in contact in the tetrahedral tetrad (Wodehouse, 1935). Although these characteristics are generally reliable for distinguishing between pollen of mono- and dicotyledons, there are, however, exceptions. In dicotyledons, pollen grains with a single aperture are found in the Piperaceae and in woody species of different ranalian families. In the Nymphaeaceae there are both genera whose pollen grains possess one aperture and those that have three (Bailey and Nast, 1943). Pollen grains with more than three apertures also exist.

Erdtman (1952) distinguishes between different types of apertures, four of which are given below.

1. *Sulcus:* an elongated furrow perpendicular to the longitudinal axis, at the pole of the grain (Fig. 180, nos. 9, 10).

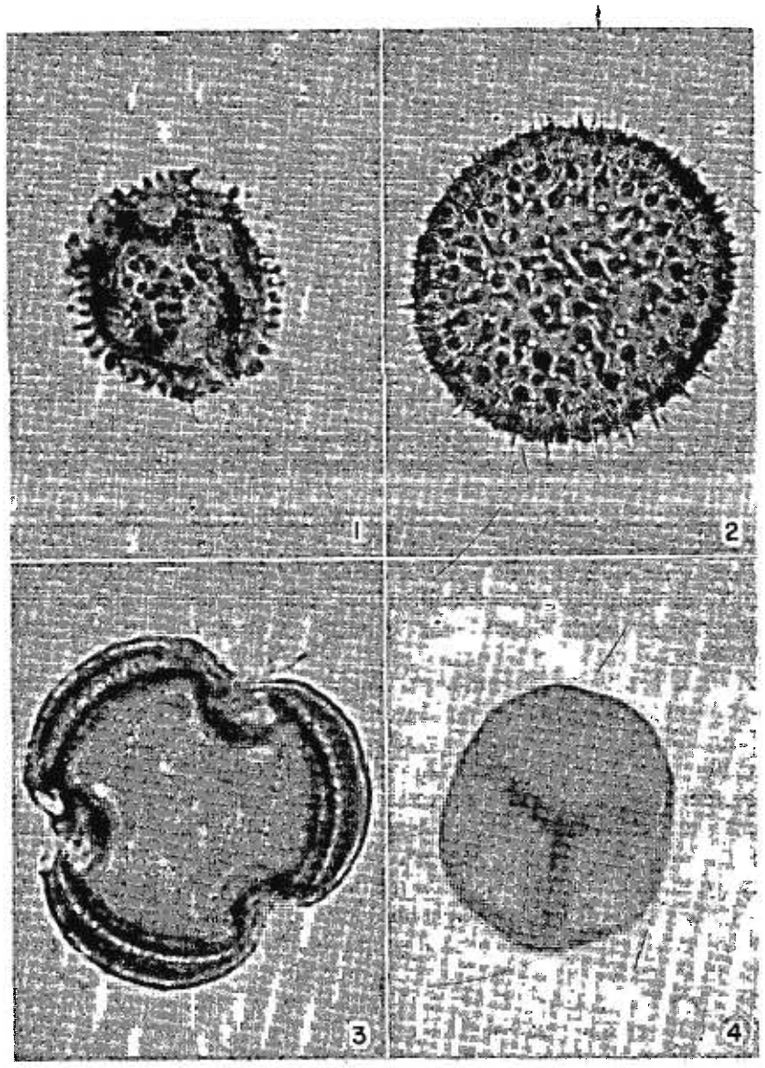


FIG. 181. Micrographs of pollen grains. 1, Pollen grain of *Sonchus oleraceus* showing the well developed ribs and spines on the sexine. ×940. 2, Pollen grain of *Lavatera cretica* in which numerous pori can be distinguished. ×405. 3, Polar view of a pollen grain of *Senecio joppensis* with three apertures. ×810. 4, *Arbutus andrachne*, tetrad of pollen grains which forms a single dispersal unit. ×770.

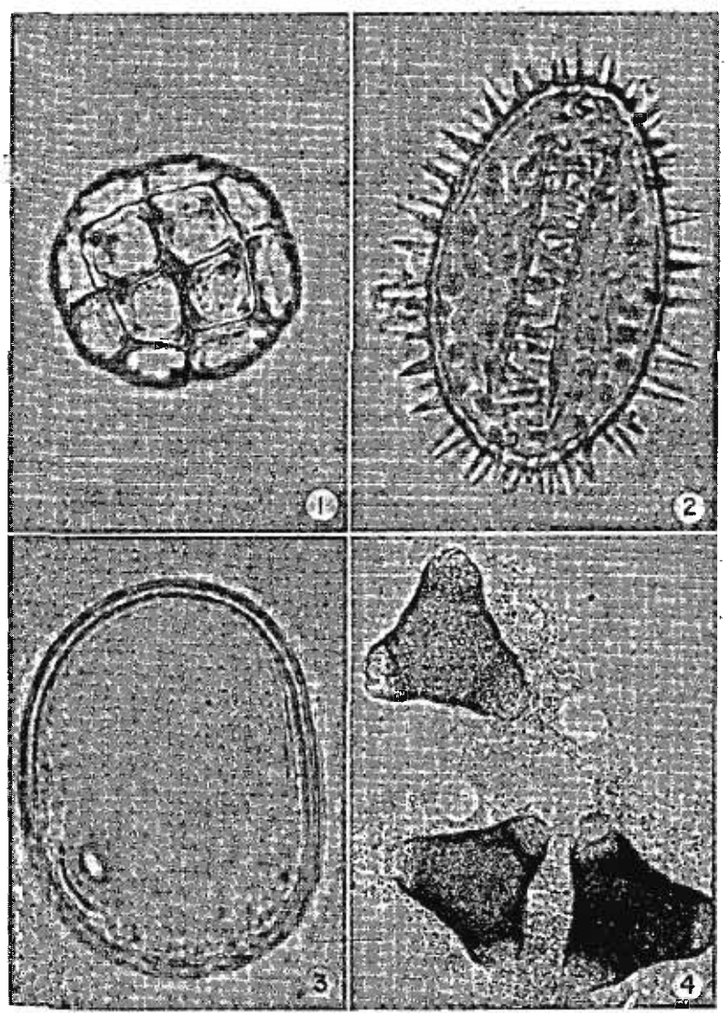


FIG. 182. Micrographs of pollen grains. 1, *Acacia*, a single dispersal unit consisting of many pollen grains. ×840. 2, Single pollen grain of *Nuphar*. ×860. 3, Single pollen grain of *Hordeum spontaneum* showing the single aperture. ×1150. 4, Three pollen grains of *Oenothera drummondii;* each grain has three apertures. ×210.

2. *Colpa:* an elongated furrow at right-angles to the equatorial plane; the ends of the furrow are directed towards the poles of the grain (Fig. 180, nos. 11, 12).
3. *Ruga:* an elongated furrow the direction of which differs from both of the above types (Fig. 180, no. 13).
4. *Porus:* a circular aperture. When the number of pori is small they occur only in the equatorial region, but if they are numerous they may occur all over the surface of the grain (Fig. 180, nos. 14–16).

A circular porus, in which the two layers of the exine are absent, may sometimes be present in the middle of the elongated, nexine-covered furrow (e.g. in *Centaurea* and other genera of the Compositae).

In *Zostera*, which is marine, the pollen grains are thread-like. This feature is apparently connected with the hydrophilous mode of pollination. Pollen grains of most plants that are of typically wind-pollinated families are smooth and dry. If most of the genera of a family are insect pollinated and only certain genera of it are wind pollinated, as, for example the genera *Artemisia* and *Ambrosia* of the Compositae, the wind-pollinated genera retain the sculptured structure typical of the entire family, but it may be developed to a lesser extent.

The size of pollen grains also varies very greatly. Erdtman classifies them, according to size, into the following groups: *perminuta*, in which the diameter is less than 10 μ; *minuta*, in which the diameter is 10–25 μ; *media*, 25–50 μ; *magna*, 50–100 μ; *permagna*, 100–200 μ; *giganta*, the diameter of which is greater than 200 μ. Very small grains may be found in *Myosotis alpestris* (2·5–3·5 μ) and *Echium vulgare* (10–14 μ); very large grains occur in *Cucurbita pepo* (230 μ) and *Mirabilis jalapa* (250 μ).

The carpel

PHYLOGENY OF THE CARPEL

Several views have been suggested concerning the homology of the carpels. It has been suggested that the carpel is of axial nature, that is, the flower may be interpreted as a system of branches. According to Wilson (1942) the carpel, like the stamen, has developed from fertile telomes. In this case the sporangia-bearing telomes fused to form a leaf-like organ which bore ovules on its margins. The involution of the margins of this hypothetical organ represents the final stage in the development of the present-day ovary which encloses the ovules.

There are some theories which are based on the independence of origin of the placenta and carpel. The *gonophyll theory*, as proposed by Melville (1961, 1962), is one such theory. According to him the ovary consists of

sterile leaves and ovule-bearing branches that are usually epiphyllous to the leaves. Each leaf together with the fertile branch is considered as a unit and is termed a *gonophyll* instead of carpel. (This theory is also applied to the stamen where the basic unit is termed an *androphyll.*) In a number of families it is supposed that the ovule-bearing branches have become ebracteate and then the ovary consists of sterile gonophylls, i.e. *tegophylls*, which alternate with the ebracteate ovuliferous branches. However, the anatomical arguments used by Melville against the classical theory of the foliar origin of the carpel are not convincing.

Another concept is the *sui generis concept* by which it is claimed that the stamens and the carpels are neither homologous with leaves nor leaflike.

The most accepted view, however, is that the carpel is homologous with the leaf. Several interpretations of this view have been given. Troll and his co-workers, on the basis of the structure and ontogeny of carpels, such as those seen in *Thalictrum* (described earlier in this chapter), have put forward the *peltate carpel theory*. According to this theory the carpel is basically a peltate organ (Puri, 1960; Eames, 1961).

According to the classical interpretation the carpel is derived from a fertile leaf, the margins of which bore ovules. The margins became involuted and fused between themselves, or with the margins of other carpels. In this way the ovules became enclosed within the locule (De Candolle, 1819; Brown, 1826; Joshi, 1947; Puri, 1960; Lorch, 1963).

A different view concerning the original position of the ovules on the carpel was suggested by Bailey and Swamy who investigated some primitive woody genera of the Ranales. The carpel of *Degeneria* (Degeneriaceae) and *Drimys* (Winteraceae), for instance, differs in many respects from the typical carpel of the angiosperms as no closed ovary, style or stigma can be distinguished. In the early ontogenetic stages the carpel of *Degeneria* can be seen, in cross-section, to be a folded organ of which the margins flare outwards and remain unfused for a long time. This type of carpel is termed *conduplicate* (Fig. 183, nos. 1–3). Swamy (1949b) observed on the flared margins and extending into the locule, even beyond the attachment of the ovules an excessive development of hairs. The cleft between the closely appressed margins is filled with interlocking hairs. On the inner side of the carpel the trichomes are small and papilla-like. According to Swamy, all the hairs together form the surface area of the stigma. When pollination takes place the pollen grains become attached to the hairy, outwardly flared margins of the open carpel. Swamy also observed that the germination tubes of the pollen grains grow into the carpel locule between these hairs and that they never penetrate the carpel tissue. In the early stages of carpel development the two rows of ovules are very remote from the true margins. The vascular supply to the ovules may be derived from the ventral or dorsal bundles, or from both. After

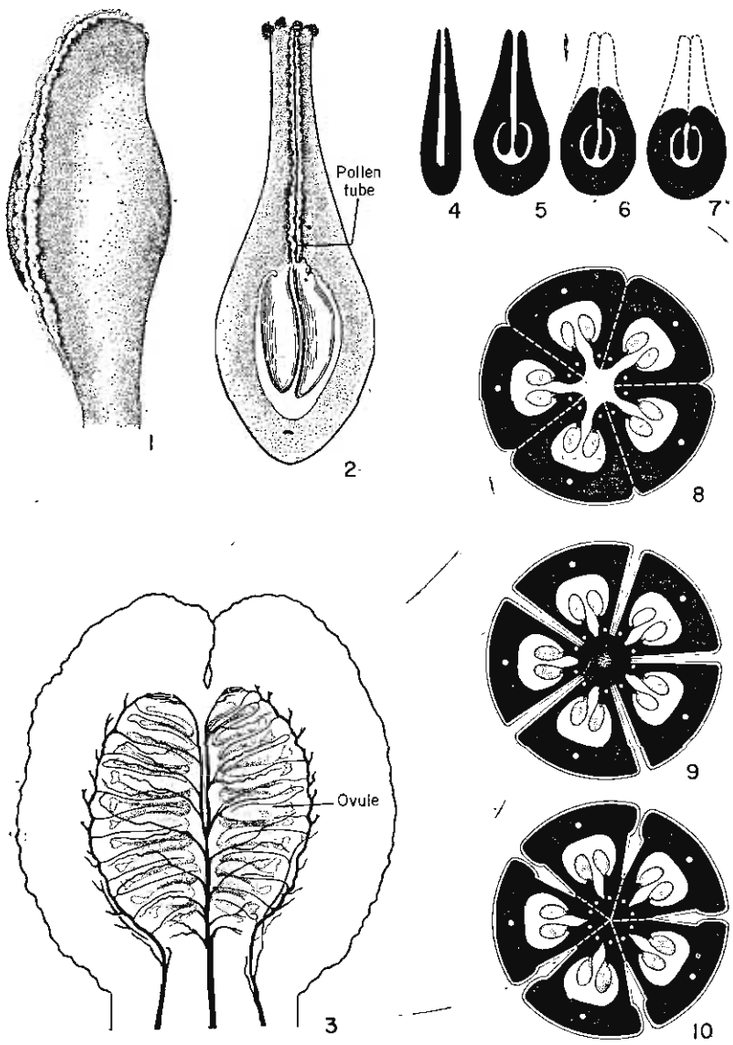


FIG. 183. 1–3, Conduplicate carpel of *Drimys piperita*. 1, Lateral view showing the stigmatic margins. 2, Cross-section showing the position of the ovules and the penetration of a pollen tube. 3, Cleared, unfolded carpel showing the general pattern of the vascularization and the source of the ovular supply. 4–7, Diagrammatic representation of the development of the present-day carpel from the conduplicate carpel. 8–10, Diagrams of cross-sections of syncarpous gynoecia showing the different ways in which fusion may take place. 8, Lateral cohesion in a whorl of open conduplicate carpels. 9, Adnation of the free margins of the conduplicate carpel to the torus. 10, Cohesion of ventral surfaces of the carpels. (Adapted from Bailey and Swamy, 1951.)

pollination and fertilization, the inner, appressed surfaces of the carpel, which are on the outside of the ovules, fuse and the outwardly flared margins remain as suberized ribs on the mature fruit.

In *Drimys* (Fig. 183, nos. 1–3), like *Degeneria*, the carpels are also folded in half and they have widened margins with stigma-like characteristics. Bailey and Swamy (1951) found that the young carpel has a stalk, and the blade-like portion of the carpel encloses two rows of ovules which are situated on the inner adaxial surface a great distance from the margins (Fig. 183, nos. 2, 3). When such a mature carpel is cleared and unfolded, it can be seen that the ovules, which are situated between the dorsal and ventral bundles, are supplied with traces from both these bundles (Fig. 183, no. 3). Here also the pollen grains reach the hairy margins of the carpels and the pollen tubes penetrate to the ovules by growing between the hairs on the inner surface of the carpels (Fig. 183, no. 2). Structure somewhat similar to this has recently been found in the genus *Cananga* of the Annonaceae (Periasamy and Swamy, 1956).

From this type of conduplicate carpel with flared margins, the present-day carpel has developed, according to Bailey, by closure and the concentration of the stigmatic margins to the upper part of the carpel only. According to Bailey, the loss of the marginal portions outside of the ovules has resulted in the impression that the carpel margins are involuted and that the placentae are marginal (Fig. 183, nos. 4–7). During the course of evolution the number of ovules was reduced, and they remained only on the lower portion of the carpel while the upper part underwent differentiation to form a style and stigma. Puri (1960), however, defends the classical concept of the ventral involution of the carpels and the fusion of the ovule-bearing margins.

The evolution of the angiosperm gynoecium has also involved the fusion between two or more carpels of a single flower. This fusion has taken place in various ways (Murray, 1945; Baum, 1948a, b, c; Leinfellner, 1950; Bailey and Swamy, 1951). The margins of the carpels may have fused to the receptacle (Fig. 183, no. 9), or they may be fused to one another along their ventral parts (Fig. 183, no. 10), or along their lateral parts. In the latter case the carpels may remain open to form a unilocular ovary (Fig. 183, no. 8). In the case of the fusion of the margins of the carpels in the centre of the ovary, the number of locules formed is equal to the number of carpels (Fig. 183, nos. 9, 10). The carpels may fuse during their ontogeny or they may be fused already at their conception (see description of the ontogeny of the syncarpous ovary, p. 367).

There are angiosperm flowers in which the structure of the ovary differs from those described above. In the Cruciferae, for instance, the ovary is divided into locules other than by the folding of the carpels. The placenta may develop on a central column which is not joined throughout its length to the wall of the ovary (*free-central placentation* as is seen, for

example, in the Primulaceae), or in a unilocular ovary the placenta may develop only at the base of the ovary (*basal placentation* as is seen, for example, in the Compositae). The fusion of the carpels may not always take place along their entire length.

In an apocarpous gynoecium each carpel has a single style. In a syncarpous gynoecium the styles may be fused to different extents (Baum, 1948d). In certain plants, e.g. in the Hypericaceae, the carpels are fused only at the base and the styles are free or almost so. In highly specialized flowers, e.g. in the Solanaceae and Oleaceae, the styles and stigmas are completely fused.

HISTOLOGY OF THE CARPEL

At the time of *anthesis*, i.e. the maturation of the anthers and ovules, or prior to it, only slight histological differentiation is observable in the ovary wall. It then consists mainly of parenchyma and vascular tissues and is covered by a cuticle-bearing epidermis. As the ovary develops into a fruit, striking histological changes take place in the ovary wall (see Chapter 20).

The stigma and style have special structures and physiological characteristics that enable the pollen grains to germinate on the stigma and the pollen tube to penetrate to the ovules. The protoderm of the stigma differentiates into a glandular epidermis, the cells of which are rich in protoplasm. This epidermis usually is papillate and covered with a cuticle (Schnarf, 1928), and it secretes a sugar-containing solution. Sometimes other cell layers below the epidermis form a glandular tissue which functions similarly to the epidermis. In many plants (e.g. *Phaseolus*, *Lilium*, *Papaver* and *Lupinus*) the epidermal cells of the stigma develop into short dense hairs (Fig. 184, no. 2; Fig. 185, nos. 1, 2), or they may develop into long, branched hairs, e.g. the Gramineae and other wind-pollinated plants (Fig. 184, no. 1).

Between the tissue of the stigma and the ovary, there is a specialized tissue through which the germinating pollen tube penetrates. This tissue provides a nutrient substrate which aids the pollen tube to grow through the style into the ovary. This tissue was termed *transmitting tissue* by Arber (1937) and this is the term that will be used here; however, this tissue is also known by various other terms. As has already been mentioned, in the most primitive dicotyledons (e.g. in ranalian families such as the Winteraceae and Degeneriaceae) the carpels do not develop styles and the pollen tubes reach the ovules by growing through the hairs present on the unfused margins of the carpels. In phylogenetically more advanced forms the carpel margins fuse, a style is developed and the stigmatic tissue is reduced to the upper portion of the style only. This tissue however,

remains in contact with the placenta by the transmitting tissue, which has features similar to those of the stigma. The style may be hollow or solid, depending on the degree of closure of the fused or free carpels. The hollow style of a syncarpous gynoecium may contain a single canal, or

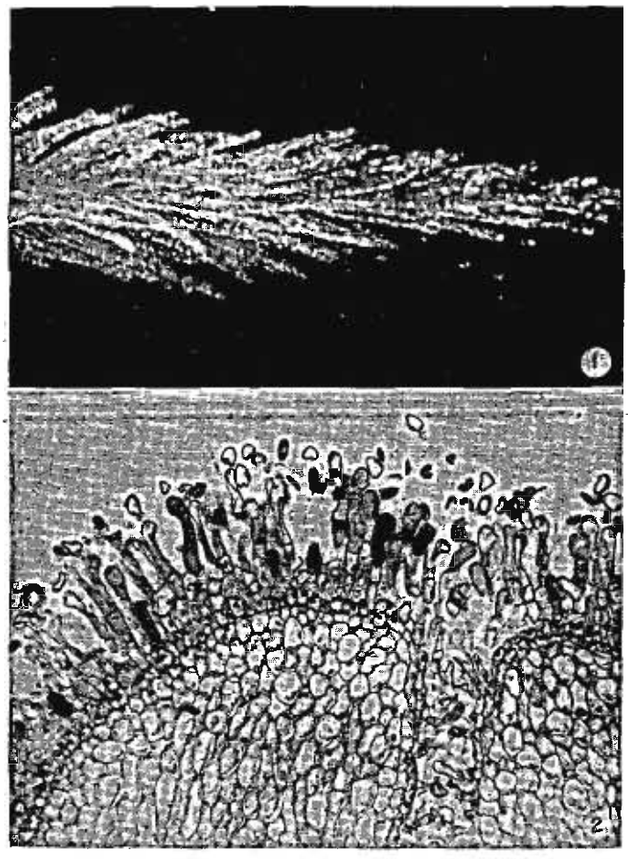


FIG. 184. 1, Photograph of portion of the feathery stigma of *Avena*. ×16. 2, Micrograph of a longitudinal section of the stigma of *Lilium* showing the multicellular hairs on its surface. ×50.

several canals, the number of which is equal to that of the carpels. The canals are lined entirely or in longitudinal strips by glandular transmitting tissue, which may be papillose (Fig. 186, nos. 1, 2). In the canal the cells of transmitting tissue are covered by cuticle. In many plants (e.g. *Cucurbita* and *Datura*) this tissue is several cell layers thick. The transmitting

tissue also covers the placenta and in certain species it is even present on the funiculus. In some plants the transmitting tissue is brought closer to the micropyle by the development of outgrowths of the placenta or stylar canal; these outgrowths have been termed *obturators* (Schnarf, 1928).

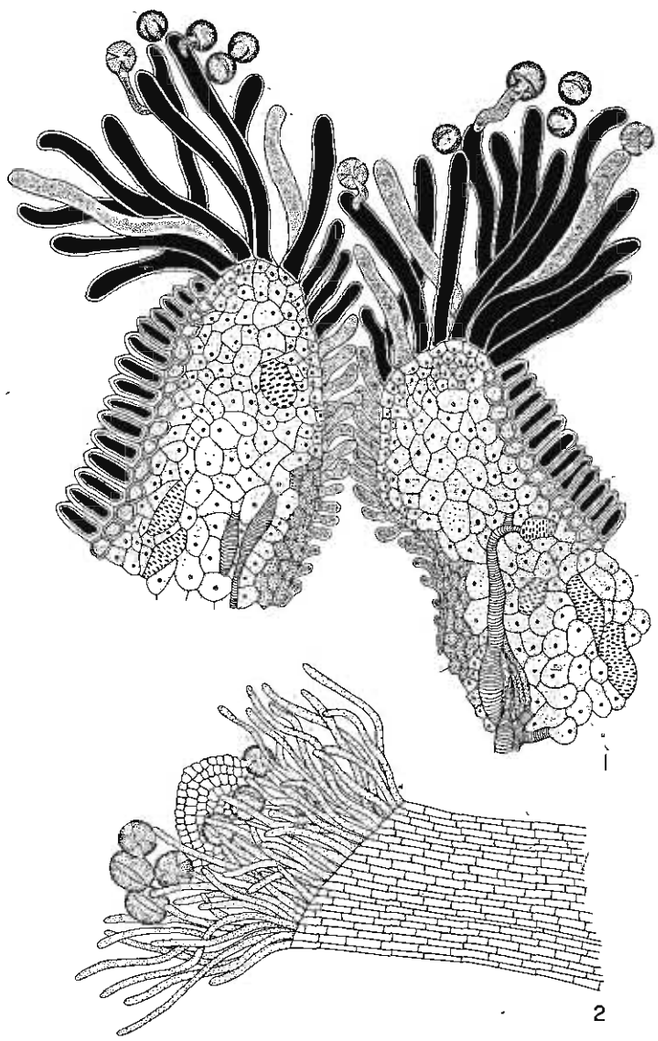


FIG. 185. 1, Diagram of a longitudinal section of the stigma of *Papaver rhoeas* in which the germination of pollen grains among the unicellular hairs on the surface of the stigma can be seen. 2, Tip of the style of *Lupinus luteus* showing pollen grains among the hairs on the stigma. (Adapted from Schoenichen, 1922.)

Ontogenetic research on the styles of *Cucurbita* and *Datura* has shown that the multiseriate transmitting tissue and the multiseriate glandular tissue of the stigma develop from the epidermal cells by periclinal division (Kirkwood, 1906; Satina, 1944). In most angiosperms the style is solid

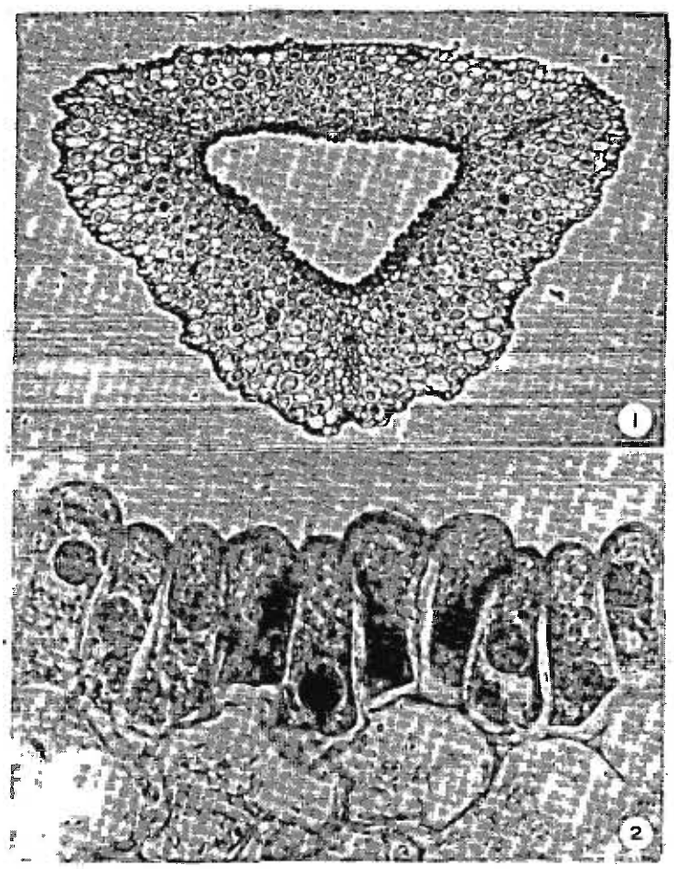


FIG. 186. 1, Micrograph of a cross-section of the style of *Lilium* in which the glandular epidermis lining the central canal can be seen. ×35. 2, Portion of the glandular epidermis, enlarged. ×500.

(Fig. 187, nos. 1, 2), and then the transmitting tissue constitutes strands of elongated cells rich in cytoplasm. The middle lamellae of these cells swell to produce a mucilaginous substance in the intercellular spaces through which the pollen tubes grow. In a syncarpous gynoecium with a single,

solid style several strands of transmitting tissue develop and these are connected to the different placentae of the ovary.

Different opinions have been expressed as to the factors directing the growth of the germinating pollen tube. There are investigators who suggest that a chemotactic attraction exists between the pollen tube and the tissues of the stigma and ovule. According to other workers the very structure and arrangement of the transmitting tissue in the style direct the growth of the pollen tube (Schnarf, 1928; Renner and Preuss-Herzog, 1943).

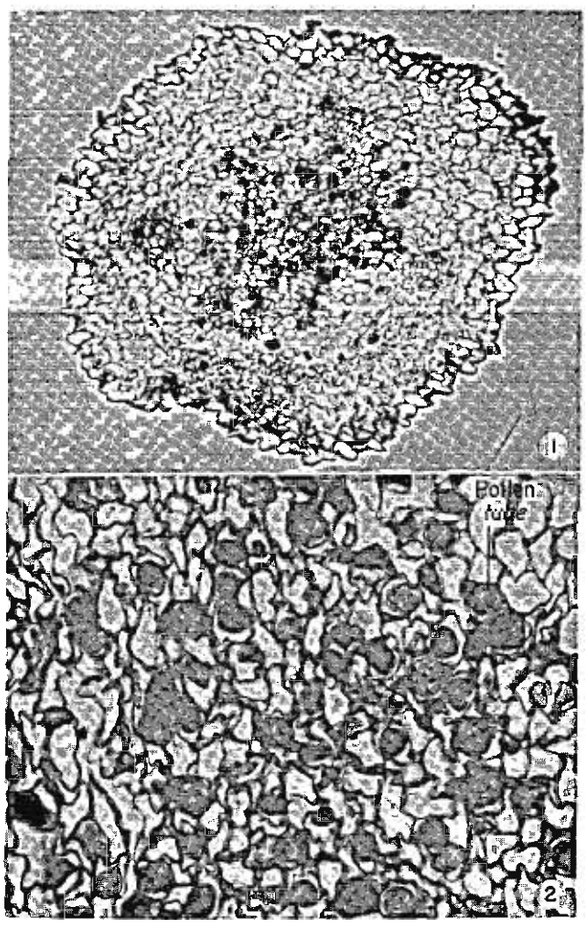


FIG. 187. 1, Micrograph of a cross-section of the style of *Oenothera drummondii* in which the pollen tubes can be seen between the cells of the central portion of the style. ×80. 2, Central portion of no. 1, enlarged. ×320.

In hollow styles the tubes of the germinating pollen grains grow between the papillae of the transmitting tissue, and, if they are absent, on the outer surfaces of the epidermal cells. In many plants the cuticle on the transmitting tissue disappears before pollination and the walls of the glandular tissue soften and swell. The pollen tubes may sometimes penetrate deeper into the transmitting tissue and grow between the cells. In solid styles the pollen tubes grow between the cells of the transmitting tissue. In grasses the pollen tube may even grow between the cells already in the stigma. On the stigma of grasses there are large multicellular hairs, consisting of several longitudinal rows of cells. The pollen tube penetrates between the inner cell rows of these hairs and from there to the transmitting tissue of the style. In the ovary the pollen tube penetrates via the transmitting tissue, which lines the ovary wall and the placenta, and eventually it reaches the ovule (Pope, 1946; Kiesselbach, 1949). Before the pollen tubes penetrate the transmitting tissue the walls of its cells swell, so that the tissue appears collenchymatous with mucilaginous walls and the connections between the cells weaken. As a result of these changes it is easy to macerate the transmitting tissue at this stage of development. The pollen tubes pass through the swollen, mucilaginous parts of the walls which they apparently digest (Schoch-Bodmer and Huber, 1947). Proofs have also been given that pollen tubes contain enzymes that are capable of disintegrating pectic substances (Paton, 1921). The protoplasts of the transmitting tissue may also be utilized by the developing pollen tube, but in many plants they may contract and die. As a result of this the style does not increase in width even when it contains very many pollen tubes.

Apart from the transmitting tissue and vascular bundles, the style consists of thin-walled parenchyma and a typical cuticle-covered epidermis, in which stomata may sometimes be found.

The ovule

The ovule consists of the *nucellus* which is surrounded by one or two *integuments*, and it is attached to the placenta by a stalk, i.e. the *funiculus*. At the free end of the ovule a small gap is left by the integuments; this opening is termed the *micropyle*. The region where the integuments fuse with the funiculus is termed the *chalaza*. A nucellar cell, usually one of those below the outermost layer at the micropylar end, differentiates into the *macro-* or *megaspore mother cell*. The nucellus is, therefore, considered to be the *megasporangium*.

Ovules may be of different form. The following two main types may be distinguished: (1) *orthotropous* or *atropous* in which the nucellar apex is in a straight line with the funiculus and is continuous with it; (2) *anatropous* ovule in which the apex of the nucellus is directed backwards toward the

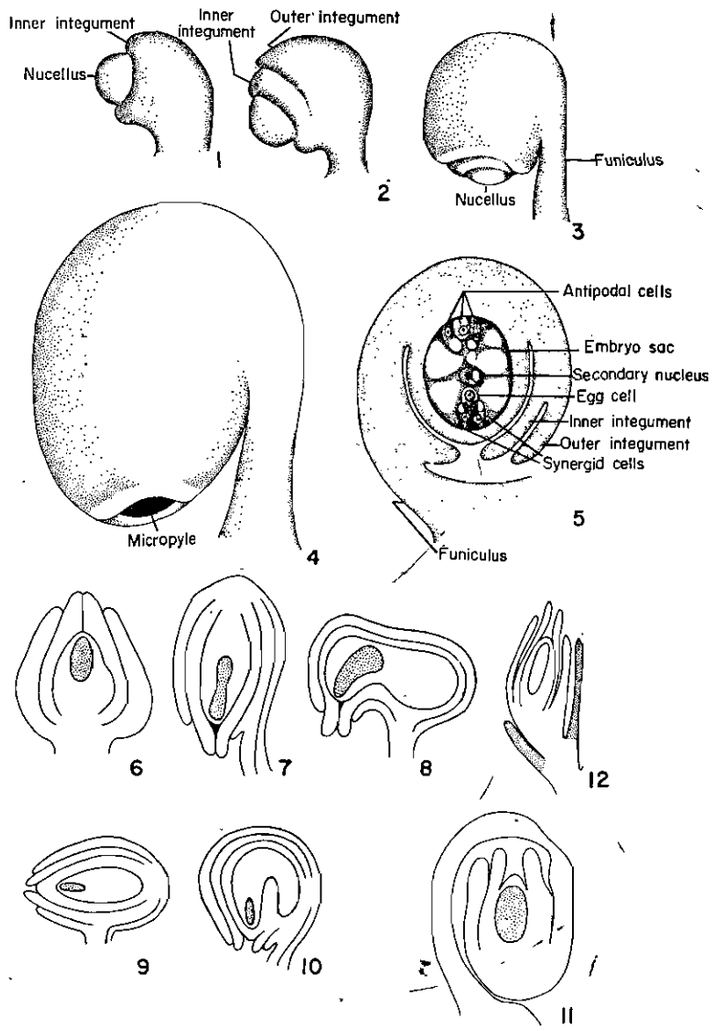


FIG. 188. 1–4, Stages in the ontogeny of an ovule. 5, Diagram of a longitudinal section of an ovule. 6–11, Different types of ovules. Embryo sacs stippled. 6, Atropous. 7, Anatropous. 8, Campylotropous. 9, Hemianatropous. 10, Amphitropous. 11, Circinotropous. 12, Longitudinal section of the ovule of *Asphodelus fistulosus* showing the development of the aril which is considered to be a third integument; aril stippled. (No. 5, adapted from Haupt, 1953; nos. 6–12, adapted from Maheshwari, 1950.)

base of the funiculus (Fig. 188, nos. 6, 7). Between these two extreme forms there are different intermediate stages in which the ovule axis is variously bent (Fig. 188, nos. 8–10). A detailed terminology has been developed for all these forms i.e. *hemianatropous*, *campylotropous* and *amphitropous* (Schnarf, 1927; Maheshwari, 1950). In the Plumbaginaceae, *Opuntia* and some other genera of the Cactaceae the funiculus is very long and it surrounds the ovule; this type of ovule is termed *circinotropous* (Fig. 188, no. 11).

The ovules develop from the placentae of the ovary. The ovule primordium originates by periclinal division of cells below the surface layer of the placenta. At first the primordium appears as a conical projection with a rounded tip. The first sporogenous cell is already distinguishable in the primordial nucellus in that it is larger than the neighbouring cells and it has a larger nucleus and denser cytoplasm. The inner integument, which is sometimes also the only one, begins to develop some distance from the nucellar apex. The initiation of this integument takes place by periclinal divisions in the protoderm. At first the integument appears as an annular ridge, which later grows toward the nucellar apex and so envelops the nucellus, except for the micropyle left at the free end of the ovule (Fig. 188, nos. 1–4). The initiation of the outer integument, if it is present, takes place in the protoderm a little lower than that of the inner integument and it develops similarly to the latter. In many plants the outer integument does not reach the micropyle. In anatropous and bent ovules the growth of the integuments is asymmetric. In plants with sympetalous flowers the nucellus is usually enveloped by a single integument, while in more primitive dicotyledons and in many monocotyledons the ovule has two integuments.

The nucellus is usually considered to be the megasporangium, but the homology of the integuments is still an unsolved problem. At the chalaza there is no differentiation between the tissues of the integuments and the funiculus.

In certain plants the structure of the ovules differs from that described above. There are ovules that lack integuments and those in which the number of integuments is greater than two. The nucellus may be fused entirely to the integuments. In some ovules the integuments grow more than usual and may even close the micropyle, while in others the integuments do not reach the nucellar tip. In certain plants, e.g. species of *Asphodelus*, a third integument develops from the base of the ovule; this structure is termed *aril* (Fig. 188, no. 12). (See also Chapter 21.)

The thickness of the nucellus in a mature ovule differs in various plants. It may be very thin—one to two cell layers surrounding the embryo sac—or it may consist of numerous cell layers. Also the integuments may vary in thickness, and the thinnest may consist of the two epidermal layers only. However, in such integuments the part closest to the micropyle may be somewhat thicker.

The entire surfaces of all the ovular parts are covered with cuticle. Thus it is possible to distinguish an *outer cuticle* which covers the funiculus and the outer integument externally, a *middle cuticle* which is double and is present between the two integuments, and an *inner cuticle* which is also double and is present between the inner integument and the nucellus.

During the development of the embryo sac the vegetative tissue of the nucellus is completely or partly destroyed, and its content is absorbed by the other parts of the ovule. In certain plants, e.g. the Centrospermae, the nucellus may, in the seed, produce a nutritious tissue which is termed *perisperm*. With the maturation of the ovule the histological structure of the integuments alters. In many plants the inner epidermis of the integument develops into a nutritious layer which is termed the *integumental tapetum*. This layer consists of tall, dark-staining cells. This feature is characteristic of those families in which the nucellus is destroyed early so that the integument is brought into contact with the embryo sac. It is a common feature in the Sympetalae.

MEGASPOROGENESIS

There are plants in which several megaspore mother cells appear in a single ovule, but usually only a single mother cell develops in each nucellus. Generally the sporogenous cell develops directly from a hypodermal nucellar cell (Fig. 189, no. 1). This cell is distinguishable from the neighbouring cells by its size, the size of its nucleus and the density of its cytoplasm. In certain plants indirect development of the sporogenous cell has been observed; the hypodermal cell first divides into an outer parietal cell, which is usually smaller, and a larger inner cell, which constitutes the primary sporogenous cell. The latter usually develops into the megaspore mother cell, and the parietal cell may divide in different planes to form numerous parietal cells. As a result of these divisions the megaspore mother cell is pushed deep into the nucellus in many plants (Fig. 189, nos. 2–7; Fig. 190, no. 1). On the other hand, in ovules where no parietal cells develop the nucellus is thin (Fig. 190, no. 3). The phylogenetic significance of the parietal cells is not clear, but it is thought that the trend, during the development of the angiosperm ovule, has been towards their loss.

The megaspore mother cell undergoes a meiotic division which is accompanied by the formation of a separate wall on each of the four megaspores. The megaspores are arranged in one row, and generally the three closest to the micropyle degenerate, and the remaining one enlarges.

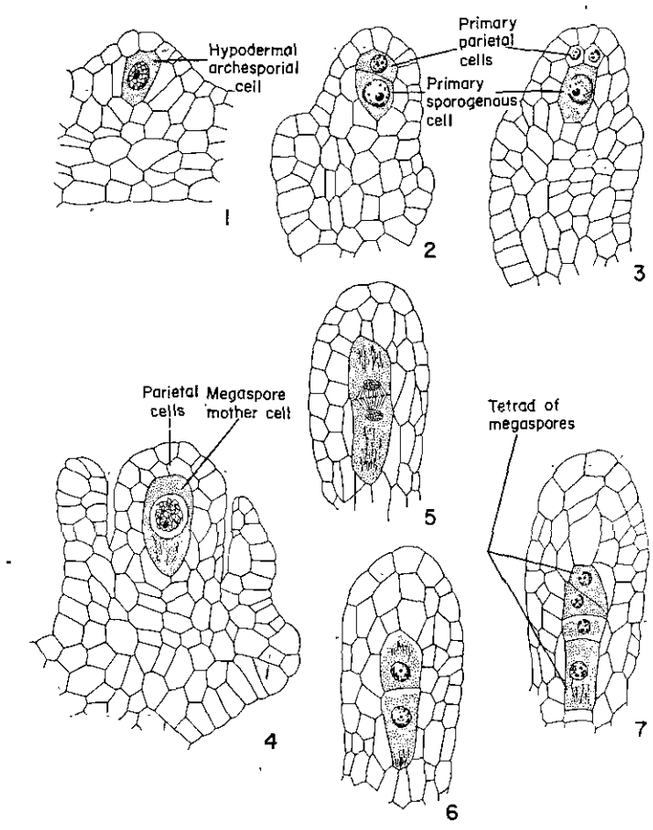


FIG. 189. Development of the megaspore in *Hydrilla verticillata*. (Adapted from Maheshwari, 1950.)

The male gametophyte

The mature male gametophyte consists of three cells resulting from two mitotic divisions which take place in the pollen grain. Prior to the first mitotic division the nucleus of the microspore (the young pollen grain) takes up a position close to the wall. The first division results in the formation of two cells, viz., the *vegetative cell* and the *generative cell* (Fig. 191, nos. 1–4). These cells lack walls. Shortly after its formation, the generative cell loses contact with the wall and becomes surrounded by the cytoplasm of the vegetative cell. Here it is seen to be oval or lens-shaped (Fig. 191, no. 6). It is at this stage that the pollen is shed from the anther although in many plants it has been found that the generative cell divides once to form

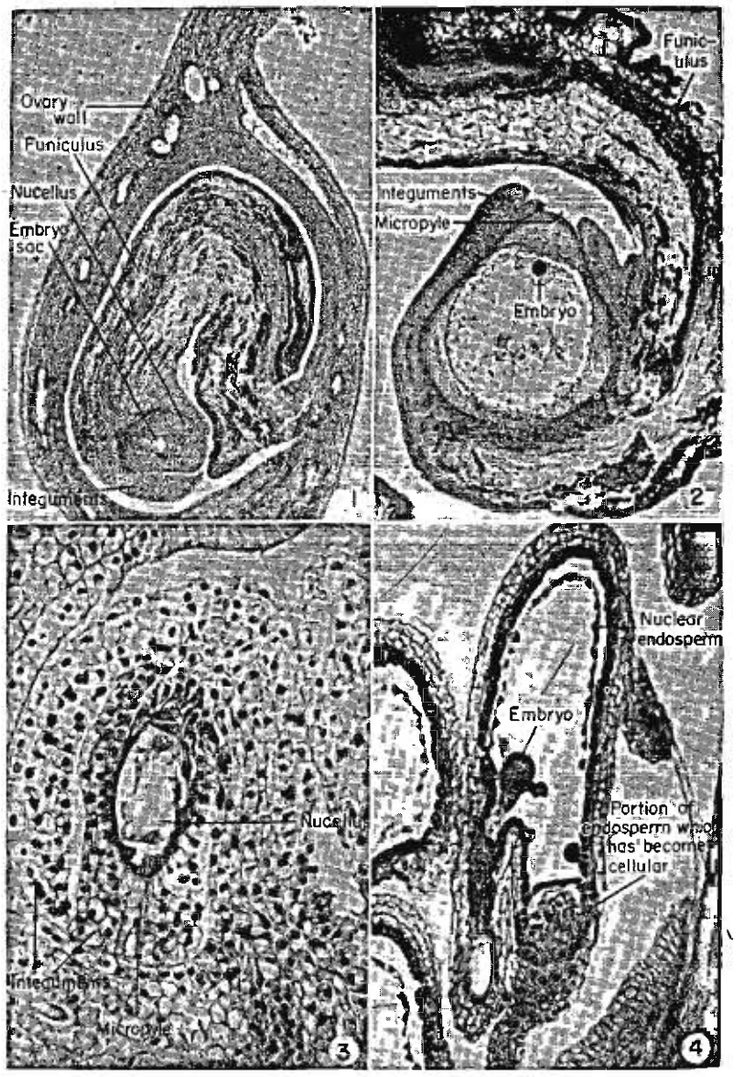


FIG. 190. Micrographs of longitudinal sections of ovules. 1, Longitudinal section of the ovary of *Pistacia vera* in which the large, folded funiculus can be seen. The ovule has a thick nucellus and the embryo sac lies close to the chalaza. ×100. 2, Longitudinal section of the ovule of *Pistacia vera* after fertilization in which an embryo can already be discerned. ×30. 3, Longitudinal section of the ovule of *Lilium candidum* before fertilization showing the very thin nucellus. Six nuclei can be distinguished in the embryo sac. ×115. 4, Longitudinal section of the ovule of

two male gametes before the opening of the anther (Fig. 191, nos. 7, 8). In other plants it has been seen (Maheshwari, 1950) that the generative cell divides only after it penetrates into the developing pollen tube (Fig. 191, nos. 9, 10).

In the past it was believed that the two male gametes move passively in the cytoplasmic stream of the pollen tube, but recently the opinion has been advanced that they move independently because it was seen that their

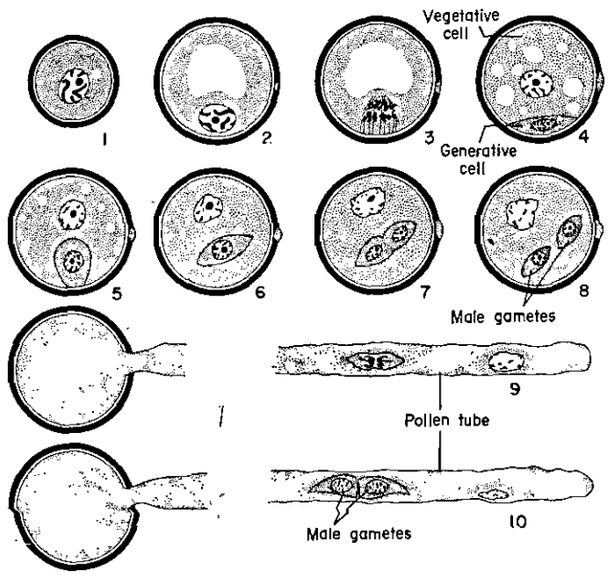


FIG. 191. Types of development of the male gametophyte in angiosperms. Explanation in text. (Adapted from Maheshwari, 1950.)

movement is not identical with that of the cytoplasm. The opinion also existed that the vegetative nucleus, which is also termed the *pollen-tube nucleus*, controls, to some extent, the penetration of the pollen tube into the ovary. However, this opinion has been questioned (Maheshwari, 1950). In certain plants the vegetative nucleus begins to degenerate a short while after its formation and, even when it is present for a long time, it does not always precede the male gametes and it may be found behind them.

The inner lamella of the wall of the pollen tube consists of callose in addition to cellulose (Tupy, 1959). The protoplast is present only in the distal part of the tube and it becomes separated from the proximal part of the tube by the formation of callose plugs, which are formed from time to time by the protoplast and, as a result, it is possible to distinguish many such plugs in a long pollen tube.

The female gametophyte

As has already been described, the megaspore enlarges and undergoes three successive mitotic divisions to give rise to the *embryo sac*, i.e. female gametophyte with eight nuclei (Fig. 188, no. 5). As a result of the extensive embryogenetic research that has been carried out in angiosperm families and genera, it has been shown that there are many deviations from the typical manner of development of the megaspores and the embryo sac. Maheshwari (1950) formulated a method of classification of the different types of development of the angiosperm embryo sac based on the following features: (1) the number of megaspores or megaspore nuclei that participate in the formation of the embryo sac; (2) the total number of divisions that take place during the formation of the megaspore and the gametophyte; (3) the number and arrangement of the nuclei and their chromosome number in the mature embryo sac.

Here, a few of the most common types are described and other types may be seen in Fig. 192.

MONOSPORIC EMBRYO SAC

Polygonum type—an eight-nucleate embryo sac

In this type four distinct megaspores develop and only one, usually that furthest from the micropyle, develops into the embryo sac. This megaspore enlarges and its nucleus divides into two nuclei, one of which moves to the micropylar pole and the other to the chalazal pole of the cell. Later, each of these nuclei undergoes two successive divisions so that eight nuclei, four at each pole, are formed. Three of the four nuclei at the micropylar pole become organized in wall-less cells to form the *egg apparatus*. At the time of fertilization the middle cell of these three constitutes the female gamete, i.e. the *egg cell*. The two lateral cells are termed *synergids*. Three of the nuclei at the chalazal pole become organized into three wall-less cells which are termed the *antipodal cells*. The number of these cells increases, in certain plants, as a result of additional divisions. The two remaining polar nuclei move into the centre of the embryo sac where they may fuse to form a diploid nucleus, termed the *secondary nucleus* (Fig. 188, no. 5).

This type of embryo sac is the most common and was first described by Strasburger in 1879.

Oenothera type—a four-nucleate embryo sac

In this type the megaspore closest to the micropyle is the one that usually remains viable and, as the result of two mitotic divisions, an embryo sac with four nuclei is formed. Three of the nuclei constitute the egg appa-

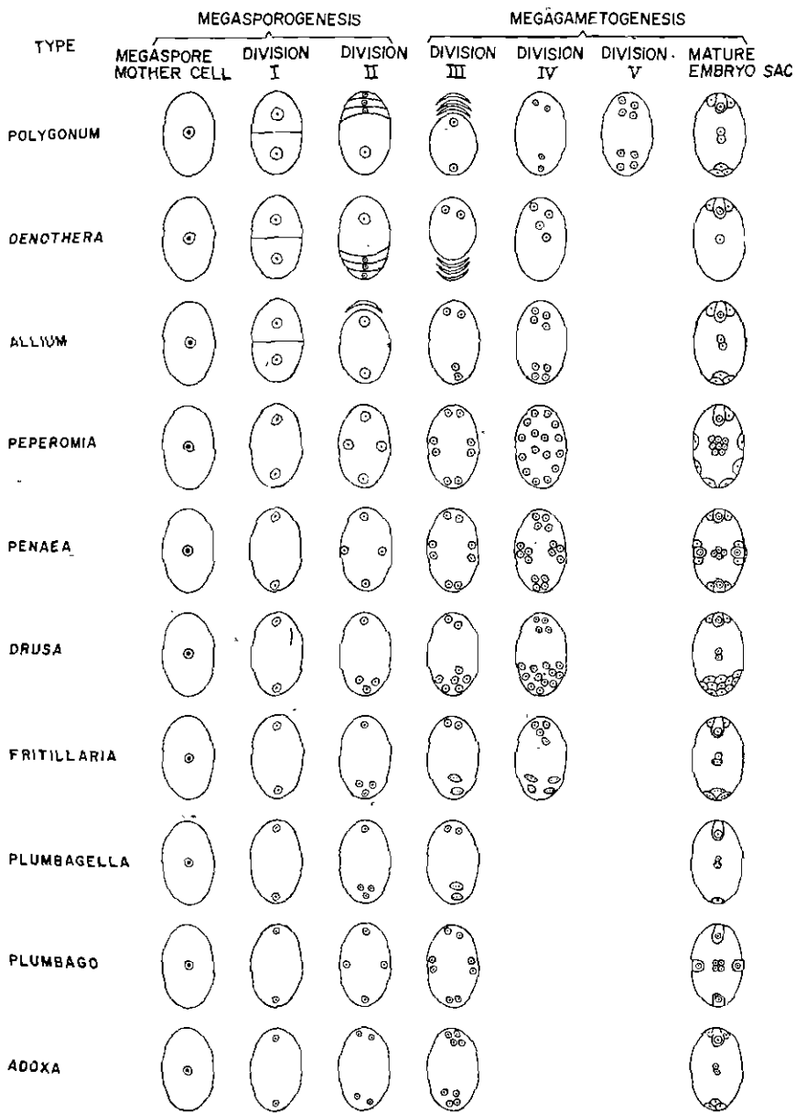


FIG. 192. Diagram showing important types of embryo sacs and their development in angiosperms. (Adapted from Maheshwari, 1950.)

ratus and the fourth forms a single polar nucleus. Fertilization in this type results in the formation of a diploid endosperm nucleus and not a triploid one as in the above type.

BISPORIC EMBRYO SAC

Allium type

The sporogenous cell divides into only two cells—*dyad*—as a result of the first meiotic division. Of these two cells, either the cell directed toward the chalaza may remain viable (*Allium*), or that closest to the micropyle (*Scilla*). The nucleus of the viable cell divides to form two haploid nuclei which are regarded as megaspore nuclei. As the result of a further two divisions eight nuclei are obtained, which become organized and arranged as in the *Polygonum* type.

There are also plants in which intermediate stages between monosporic and bisporic embryo sacs can be found.

TETRASPORIC EMBRYO SAC

Adoxa type

This type is found, among others, in *Sambucus*, *Ulmus* and *Tulipa*. In this type, as a result of the meiotic division of the sporogenous cell, four nuclei, which lie free in the cytoplasm of the young embryo sac, are obtained. After an additional mitotic division a total of eight haploid nuclei, which organize in the typical way, are obtained.

Fritillaria type

This type is found in many genera among which are *Lilium* and *Fritillaria*. Here three of the four nuclei obtained from the meiotic division move to the chalazal pole of the young embryo sac, and the fourth is found at the micropylar pole. The latter nucleus divides in the usual manner, and the other three nuclei fuse to form a single triploid nucleus, which immediately divides into two. As a result of this, a second four-nucleate stage is obtained in which there are two haploid nuclei at the micropylar pole and two triploid ones at the chalazal pole. Later a third and last division takes place, which gives rise to four haploid nuclei at the micropylar pole and four triploid ones at the chalazal pole. The final arrange-

ment in the mature embryo sac is a normal haploid egg apparatus, three triploid antipodal cells, and a tetraploid secondary nucleus which results from the fusion of a haploid and a triploid polar nucleus.

Nectaries

Nectar, a sugar-containing solution, is secreted by nectaries which most frequently occur on insect- and bird-pollinated plants. *Nectaries* may consist of specialized tissue which differs histologically from the neighbouring tissues, i.e. *structural nectaries*, or they may consist of non-specialized tissues, i.e. *non-structural nectaries* (Zimmermann, 1932; Frey-Wyssling and Häusermann, 1960). Non-structural nectaries have been observed in many plants and on various organs, e.g. on the leaves of *Pteridium aquilinum* and *Dracaena reflexa*; on the floral bracts of *Sansevieria zeylanica*; on the sepals of *Paeonia albiflora*; and on the tepals of *Cattleya percivaliana*.

Structural nectaries may form special outgrowths or they may occupy delimited regions of the surface layers of the various plant organs on which they are formed. Such nectaries usually consist of excretory epidermis or trichomes and a differentiated *nectariferous tissue* below it. At the nectariferous tissue there is a well developed vascular supply (Frei, 1955; Frey-Wyssling, 1955). Sometimes no nectariferous tissue is developed and then only a secretory epidermis is present. Which of the above two types of nectaries is the more advanced is still to be clarified.

LOCATION OF NECTARIES

Nectaries may develop on all parts of the plant. Nectaries that are connected with the floral organs are termed *floral nectaries*, and those developing on the vegetative parts of the plant, *extrafloral nectaries*. Extrafloral nectaries may be found on different organs such as petioles (*Passiflora*) stipules (*Vicia faba*), teeth of leaves (*Ailanthus altissima*, *Prunus* and *Impatiens*), and on the margins of the cyathia of *Euphorbia*. Extrafloral nectaries are regarded, phylogenetically, as more primitive than floral nectaries (Frey-Wyssling, 1933). This chapter will deal only with floral nectaries.

Many workers used the form and location of the nectary as taxonomic characteristics by which they attempted to support their theories regarding the phylogenetic relationship between species, genera and families (Bonnier, 1879; Schniewind-Thies, 1897; Knuth, 1898–1905; Porsch, 1913; Daumann, 1928, 1930a, b, c, 1931a, b; Brown, 1938). It has been shown (Fahn, 1953b) that a phylogenetic trend of development, expressed by the acrocentripetal change of position of the nectaries within the flower, i.e. from the sepals towards the ovary and up to the style exists. The following

classification of the floral nectaries, according to their location, has been suggested (Fahn, 1952, 1953b).

1. *Perigonial nectaries*—those developing on the perianth:
   (a) close to the base of the perianth parts (*Ranunculus, Leontice Althaea, Hibiscus, Fritillaria*);
   (b) in spurs formed by the perianth parts (*Garidella, Pelargonium, Tropaeolum, Centranthus*).

2. *Toral nectaries*—those developing on the receptacle:
   (a) *marginal*—between the base of the sepals and petals (*Capparis, Reseda*);
   (b) *annular*—the nectary forms a ring or a part of one on the surface of the receptacle:
      (i) between the sepals and ovary (*Grevillea*);
      (ii) between the stamen bases (*Polygonum*, Cruciferae);
      (iii) a ring consisting of small swellings between the stamens and around the ovary (*Cistus*);
      (iv) a shallow or concave ring between the stamens and the ovary base (*Anagyris, Caesalpinia, Ceratonia, Cercis siliquastrum, Robinia, Prunus, Cydonia, Rubus, Punica*); or between the stamens and the styles when the ovary is inferior (*Eucalyptus*, Cucurbitaceae, Campanulaceae, Dipsaceae);
      (v) a prominent ring around the ovary base (Boraginaceae, most of the Labiatae, Bignoniaceae, *Citrus*);
   (c) *tubular*—the nectary lines a spur which is sunk into the "pedicel" (*Bauhinia*).

3. *Staminal nectaries*—those related to stamens:
   (a) on the filaments (*Colchicum, Laurus, Dianthus, Silene*); or in the tube formed by the fusion of the filaments (many plants of the Papilionaceae);
   (b) on an appendage of the connective (*Viola, Asclepias*).

4. *Ovarial nectaries*—those developing on the ovary wall:
   (a) on all the free surface of the carpels (*Tofieldia palustris, Sarracenia*);
   (b) on the ovary base (*Gentiana*);
   (c) *septal*—on the partitions of monocotyledonous syncarpous ovaries (Liliaceae, Musaceae, Amaryllidaceae, Iridaceae).

5. *Stylar nectaries*—those developing at the base of the style:
   (a) common to the base of the style and stylopodium (Umbelliferae);
   (b) only on the base of style (in most insect-pollinated species of the Compositae such as *Helianthus, Senecio* and *Calendula*).

STRUCTURE OF NECTARIES

The cells of the nectariferous tissue usually contain dense cytoplasm in which abundant granules may be distinguished (Caspary, 1848; Bonnier, 1879; Fahn, 1952). The cells of floral nectariferous tissue are usually more or less cubical (Fahn, 1948). In extrafloral nectaries a nectar-excreting epidermis with palisade-like cells (Fig. 193, no. 1) can be found (Agthe, 1951).

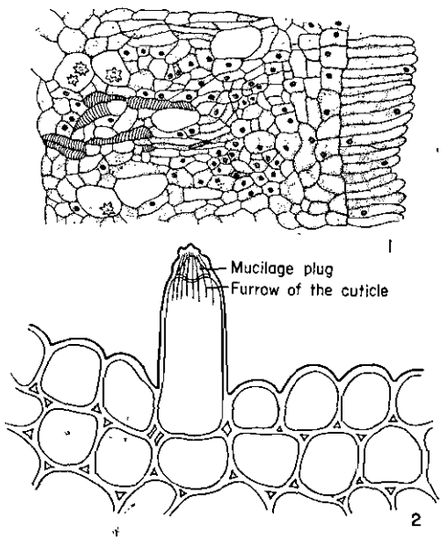


FIG. 193. 1, Portion of a cross-section of the nectariferous gland on the base of the petiole of *Ricinus communis* showing the palisade-like epidermis and the vascular tissues which penetrate deeply into the nectariferous tissue. 2, Portion of the nectariferous tissue which lines the spur of *Tropaeolum*, showing a unicellular nectar-secreting cell. (No. 1, adapted from Agthe, 1951; no. 2, adapted from Schoenichen, 1922.)

The histological differences in nectaries are mainly connected with the manner of secretion of the nectar. On this basis different types of nectariferous tissue have been distinguished (Behrens, 1879; Fahn, 1948).

1. Nectariferous tissue in which the excretion is by diffusion through thin-walled epidermal cells. These cells are not covered with cuticle although cuticle is generally present on the neighbouring epidermal cells. The cells below the epidermis have a dense, usually yellow cytoplasm and the epidermal cells are transparent.

2. Nectariferous tissue in which the excretion is by diffusion from thin-walled epidermal papillae. These papillae are unicellular, fairly large, and they are formed by the elongation of epidermal cells. In the cytoplasm of

the papillae, grains, consisting of dextrose and other carbohydrate substances, are found. The secretion is through the thin walls and starts at the tip of the papillae or on their sides.

3. Nectariferous tissue in which the excretion is from the tips of uni- or multicellular hairs, the outer walls of which are covered by cuticle. The wall at the tip of the hair thickens by gradual swelling until three layers can be distinguished in it. Of these, the middle and thickest layer is mucilaginous and it further increases in thickness at the expense of the volume of the cell contents. Eventually the outer wall layer, together with the cuticle, ruptures and the mucilage, saturated with nectar, is extruded (Fig. 193, no. 2).

4. The nectar is excreted through stomata that are specially modified for this function. The shape of these stomata is generally similar to that of ordinary stomata and a substomatal chamber is present. However, these stomata remain open permanently. The epidermal cells and also the guard cells are covered by cuticle. The nectar is secreted from the deep-lying layers of nectariferous tissue, through the intercellular spaces, substomatal chambers and stomata.

5. The nectar is excreted as a result of the rupture of the cuticle, which is brought about by the swelling of the outer wall. In nectaries of this type the outer walls are covered by a thick cuticle, and three layers, two dark and one light, can be distinguished in the outer walls. The wall layer closest to the cuticle becomes mucilaginous at the time of the secretion and, as a result of its swelling, the cuticle is ruptured and the nectar-saturated mucilage is extruded onto the surface of the nectary.

An opinion exists that the submicroscopical structure of the cuticle on the nectariferous tissue differs from that of the cuticle on the other epidermal cells of the plant (Frey-Wyssling, 1933). Further investigations, involving electron microscopy, of the outer walls and cuticle of the epidermis of nectaries will, no doubt, reveal important features that will enable a better understanding of the manner in which the secretion passes through these structures.

Different types of nectary structure are described as follows.

Garidella unguicularis

The nectariferous tissue in this flower is found at the petal knee, i.e. in that place where the blade passes into the claw (Fig. 194, nos. 1–4). This knee forms a type of spur, the aperture of which is closed by a cover connected to the claw of the petal (Fig. 194, nos. 2, 3). Within the aperture *of the spur, on the side of the petal-blade and close to the cover margins,* are brushes of unicellular hairs, which thus block the spur aperture more tightly. The tongue of the bee is pushed into the spur, which contains the

nectar, through the above-mentioned hairs. The nectariferous tissue consists of layers of extremely small cells which are strikingly different from the neighbouring cells. The outer thickened walls of the epidermal cells

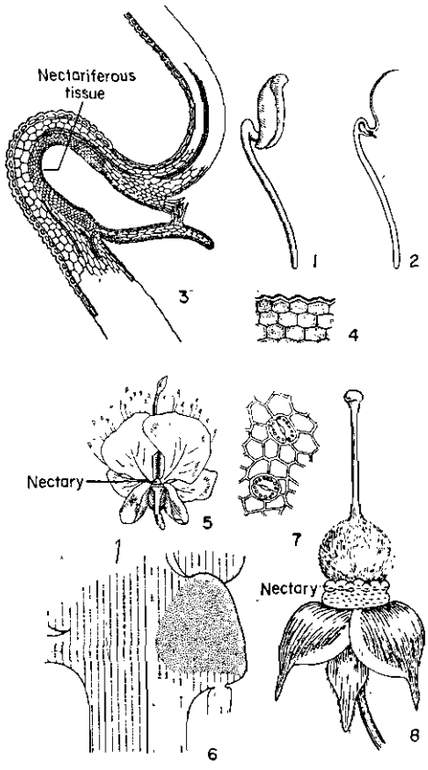


FIG. 194. Nectaries. 1–4, *Garidella unguicularis*. 1, An entire petal. 2, Median longitudinal section of a petal. 3, Knee portion, in longitudinal section, enlarged to show the position of the nectariferous tissue. 4, Outer portion of nectariferous tissue showing the thick cuticle on the epidermis. 5–7, *Capparis sicula*. 5, General aspect of the flower after the removal of the sepals, in which the nectar collects, to show the triangular nectary. 6, Median longitudinal section of the receptacle in the region of the nectary (stippled). 7, A portion of the epidermis over the nectary showing the modified stomata through which the nectar is secreted. 8, *Cistus villosus*. Flower from which the petals and stamens have been removed to expose the nectary.

are covered by cuticle and form low papillae. The contents of the epidermal cells do not differ from those of the other nectariferous cells, which are granular and yellow in colour. The vascular bundles come into contact with the nectariferous tissue (Fig. 194, no. 3).

Capparis sicula

Externally the nectary appears as a white triangle on the margin of the torus (Fig. 194, no. 5). The apex of the triangle is directed towards the stamens and the base is opposite that of the largest, boat-shaped sepal, in which large quantities of nectar accumulate. The other two sides of the triangle are bordered by two petals of which the margins of the basal portions, where they border the nectary, are somewhat thickened and folded downwards on themselves so as to form a narrow slit between them. The adjacent margins of the upper portions of these petals overlap one another. In order to suck the nectar from the boat-shaped sepal the bee stands on the two petals, separates them, and pushes its tongue through the slit formed by the lower margins of the petals (Fig. 194, no. 5). In a median section of the flower (Fig. 194, no. 6) it can be seen that the nectariferous tissue penetrates deeply into the receptacle. The epidermis of the nectariferous tissue is covered by a very thin cuticle and it contains many elliptical stomata (Fig. 194, no. 7).

Colchicum ritchii

The nectariferous tissue is found on the basal portion of the filaments (Fig. 195, no. 1), which are adnated to the tepals. Externally the nectari-

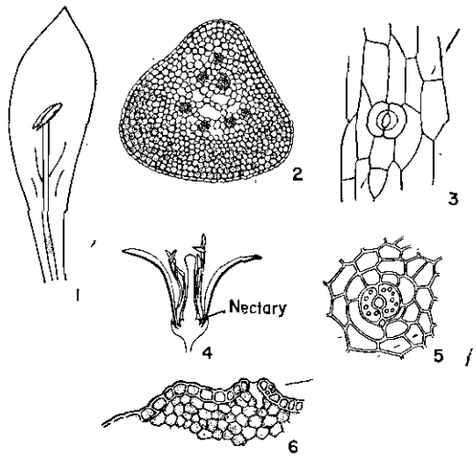


FIG. 195. Nectaries. 1–3, *Colchicum ritchii*. 1, An entire tepal with adnated stamen. Nectariferous tissue at the base of the filament, stippled. 2, Cross-section of the filament in the region of the nectary. 3, Portion of the epidermis of the nectary in surface view. 4–6, *Citrus limon*. 4, Median longitudinal section of an entire flower, showing the position of the nectary. 5, Portion of the epidermis of the nectary. 6, Portion of a cross-section of the nectary showing a modified stoma, and canal below it through which the nectar is secreted.

ferous tissue appears as a yellow band surrounding the base of the filament. A swelling of the petal is present on each side of the stamen; the nectar accumulates between these swellings. In a cross-section of the filament transparent epidermal cells overlying a thick region of rounded cells with granular contents can be seen in the region of the nectary (Fig. 195, no. 2). The central portion of the section is occupied by vascular bundles and parenchymatous tissue in which there are many large intercellular spaces. Small intercellular spaces are also present in the nectariferous tissue. The nectariferous tissue on that side of the filament facing the petal is much thicker and its colour is darker (yellow–brown) than that on the free side. There is no discernible development of the cuticle on the epidermal cell walls. Large, circular stomata are present on the surface of the nectary (Fig. 195, no. 3).

Citrus limon

The nectary in *Citrus* forms a ring around the base of the ovary (Fig 195, nos. 4–6). Stomata with wide apertures are present on raised portions of the ring. In tangential section of the nectary the stomata are seen to be strikingly rounded in shape (Fig. 195, no. 5), and in cross-section it is seen that the substomatal chambers are fairly deep and that the cells below the epidermis are small and compact. The epidermis itself is seen to consist of small cubical, thick-walled cells which are covered by a relatively thin cuticle. All the cells of the nectary, including those of the epidermis, have a granular colourless content. Sometimes these cells may also contain crystals, as is a common feature in all other tissues of *Citrus*.

Cistus villosus

This plant is usually thought to be a pollen-producing plant only, but it is also frequently visited by bees that collect nectar. The upper portion of the receptacle is swollen around the bases of the innermost stamens, especially on the side closest to the ovary, and forms the nectariferous tissue (Fig. 194, no. 8). The epidermis of the nectary contains stomata and is apparently without cuticle.

Bauhinia purpurea

In this plant the nectariferous tissue lines a tubular cavity which has been formed either by the depression of the receptacle on one side of the gynophore, or by the fusion of the basal portions of the perianth and

stamens (Fig. 196, no. 2). In a cross-section of the receptacle (Fig. 196, no. 1) two whorls of vascular bundles can be seen as well as the large central bundle of the gynophore. The epidermis lining the above cavity

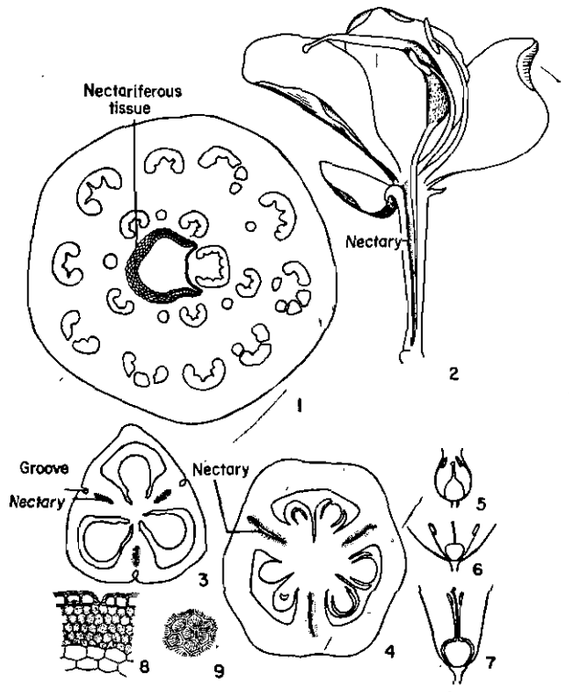


FIG. 196. Nectaries. 1 and 2, *Bauhinia purpurea*. 1, Cross-section of the flower in the region of the nectary. The vascular bundles of the various floral organs are shown in the tissues around the nectary. 2, Median longitudinal section of the flower showing the position of the tube-like nectary. 3, Diagram of a cross-section of the ovary of *Muscari racemosum*. 4, Diagram of a cross-section of the ovary of *Asphodeline lutea*. 5–7, Diagrams of longitudinal sections of flowers. 5, *Muscari*. 6, *Allium*. 7, *Asphodelus*. 8 and 9, *Bupleurum subovatum*. 8, Portion of a cross-section of the epidermis and underlying nectariferous tissue. 9, Surface view of portion of the epidermis.

is thin-walled, fairly transparent, and consists of very small cells; there are no stomata in this epidermis. The nectariferous tissue, which consists of small cells with yellow, granular contents, is found below the entire epidermis, with the exception of that part that overlies the gynophore.

Bupleurum subovatum

As in all the Umbelliferae, the nectariferous tissue in this plant is found on the upper portion of the inferior ovary, i.e. on the stylopodium. In a cross-section of the nectary (Fig. 196, no. 8) the epidermis is seen to be transparent and consists of thick-walled cells covered by a thick ridged cuticle (Fig. 196, no. 9). This epidermis contains very small, sunken stomata. Below the epidermis there is a thick region of compact cells with granular contents. These nectariferous cells are strikingly different from the neighbouring parenchyma cells below them.

Some species with septal nectaries

In *Muscari racemosum*, for example, the septal nectary consists of three very compressed cavities, one in each of the three partitions of the ovary, which are lined by nectariferous tissue (Fig. 196, no. 3). Parallel to each cavity, on the external surface of the ovary, is a groove which is connected to the cavity at the upper portion of the ovary. In this species the nectar, secreted by the nectariferous tissue into the cavities, fills them, whence it overflows down the grooves and accumulates between the base of the ovary and the tepals. In *Allium*, the secretion of the nectar is as in *Muscari*, but it accumulates between the base of the ovary and the stamens (Fig. 196, nos. 5, 6). In *Asphodelus* and *Asphodeline* there are no grooves on the ovary wall (Fig. 196, no. 4) and the three nectariferous canals open at the top of the ovary. In these genera the filaments are bent at their bases so that they cover the ovary (Fig. 196, no. 7). This results in the formation of a capillary cavity between the ovary and the filaments. The nectar, which is extruded at the top of the ovary, is drawn by capillary force to the ovary base. Without this structure the nectar would spill out of the flower because of its horizontal or pendulous position in these genera.

Branches of vascular bundles come close to the nectariferous tissue, but they do not penetrate into it. These branch endings may consist of both xylem and phloem, or of only one type of tissue. According to Agthe (1951), the sugar concentration of the nectar is correlated with the type of vascular tissue that reaches the nectariferous tissue. Thus, he claims that, in *Euphorbia pulcherrima* and *Abutilon striatum* in which the sugar concentration of the nectar is high, the endings of the terminal branches closest to the nectary consist only of phloem, while in *Ricinus communis*, *Fritillaria imperialis* and *Ranunculus acer*, in which the sugar concentration of the nectar is low, the branch endings consist of equal amounts of xylem and phloem, or of a larger proportion of xylem. One of the fundamental differences between nectaries and hydathodes is that the branch endings of the vascular bundles that come into contact with the hydathode tissue consist of tracheary elements only.

NECTAR SECRETION

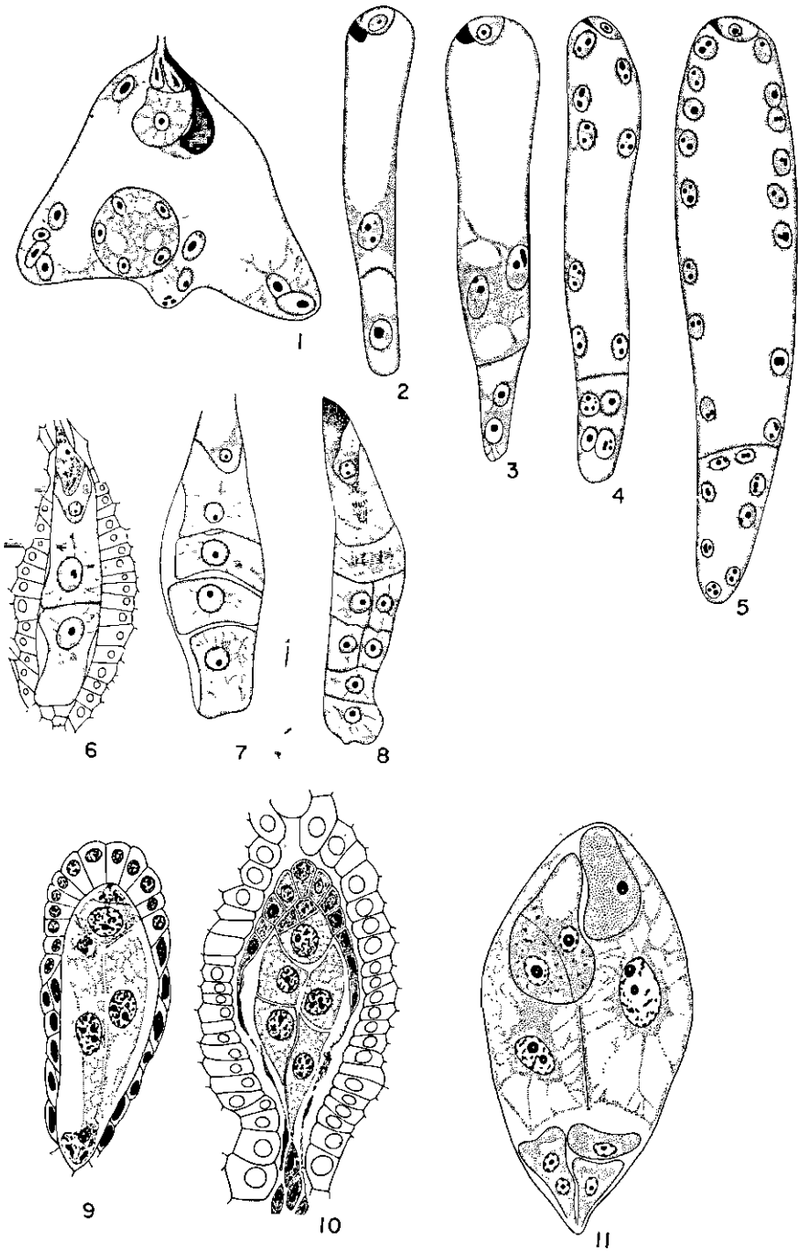
Sucrose, glucose and fructose have been found to be among the most common constituents of nectar. Apart from these, mucilages, proteins and organic acids are also sometimes found in nectar. The acids are responsible for the low pH found in the nectar of some plants (Beutler, 1930; Fahn, 1949). Zimmermann (1954) found transglucosidases in the nectar of *Impatiens*. The concentration of nectar varies from 3 to 87%. It was found that the output of fresh nectar, and the amount of the dry matter in it, produced by different species in a 24 hr period varies considerably. The variation per flower may be between 0·13 mg fresh nectar and 0·10 mg dry matter, to 268 mg fresh nectar and 47 mg dry matter (Fahn, 1948, 1949). In unisexual flowers there are striking differences in the amount of nectar secreted by the male and female flowers. Among the external factors that increase the amount of nectar secretion, temperature and soil moisture should be mentioned; these factors influence the general physiological activity of the plant (Fahn, 1948, 1949). The sugar content in the plant is the most important internal factor that influences nectar secretion (Helder, 1958).

From the work of some investigators (Frey-Wyssling and Agthe, 1950; Agthe, 1951; Zimmermann, 1953), it became clear that there is a correlation between the translocation of substances in the phloem and the secretion by the nectariferous tissue. The above workers attempt to explain the mechanism of secretion on the basis of this relationship. According to them the contents of the sieve elements is extruded through the nectariferous tissue by the excess pressure in the sieve elements. The second possibility, that the nectar solution is secreted by an active mechanism which takes place in the nectariferous tissue, appeared less feasible to the above workers, but today, in the light of the most recent research on sugar uptake, it seems that this second possibility is more correct (Helder, 1958).

Abscission of floral parts

Petals, stamens, and sometimes other floral organs may be shed as a result of the formation of a separation layer. The cells of this tissue are distinguishable from those of the neighbouring ones by their more circular or cubical shape (Pfeiffer, 1928). In flowers the tissue of the separation layer is less well developed than in leaves of woody dicotyledons (see Chapter 12), and it appears only shortly before the floral parts are shed.

In plants with unisexual flowers, usually entire male flowers are shed after the release of the pollen (Yampolsky, 1934). Sometimes entire male inflorescences are shed, e.g. *Morus*, *Casuarina* and *Ceratonia*. Female and bisexual flowers that fail to be fertilized may also be shed.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Formation of endosperm and embryo

FERTILIZATION

As has already been described above, the pollen grain germinates and produces a pollen tube on the stigma. The pollen tube, which carries within it the two male gametes, passes through the style and reaches the ovule. In most plants the pollen tube penetrates into the ovule via the micropyle. In some plants the pollen tube penetrates through the chalazal region, i.e. *chalazogamy*. This feature occurs, for example, in *Casuarina* and species of *Pistacia*. After its entry into the ovule the pollen tube penetrates into the embryo sac where it may pass between the synergids and the embryo-sac wall or between the egg cell and the synergids. Usually one of the synergids is destroyed as a result of the penetration of the pollen tube. Later the tip of the pollen tube ruptures and the two male gametes, sometimes together with remnants of the vegetative cell, enter into the cytoplasm of the embryo sac (the female gametophyte). One of the male gametes fuses with the egg cell, and the second fuses with the two polar nuclei or with the secondary nucleus if the latter two have fused previously. This process of fertilization is termed *double fertilization*. As a result of the fusion of a male gamete with the egg cell a *zygote*, which later develops into the *embryo*, is formed and, as a result of the fusion of the second male gamete with the polar nuclei or with the secondary nucleus, the *endosperm* is formed.

DEVELOPMENT OF THE ENDOSPERM

The endosperm is a storage tissue which provides nutrition for the embryo and the young seedling. In certain plants, e.g. *Pisum*, *Phaseolus* and *Arachis*, the entire endosperm tissue is digested by the developing embryo. Generally, in the seeds of such plants the cotyledons thicken and they store reserve substances which provide nutrients for the young seedlings. In other plants, e.g. *Ricinus* and plants belonging to the Gramineae, the endosperm tissue is still present at the time of germination.

The endosperm develops from mitotic division of the *endosperm nucleus*, which results from the fusion of one of the male gametes with the two

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FIG. 197. 1, Embryo sac of *Musa errans* which has a nuclear endosperm. 2–5, Embryo sac of *Eremurus himalaicus* showing the development of a helobial endosperm. 6–8, Development of the cellular endosperm in *Villarsia reniformis* in which the first divisions are transverse. 9–11, Cellular endosperms in which the first divisions are longitudinal. 9 and 10, *Adoxa moschatellina*. 11, *Centranthus macrosiphon*. (Adapted from Maheshwari, 1950.)

polar nuclei or with the secondary nucleus. This division usually precedes that of the zygote. The further development of the endosperm differs in the various groups of plants, and the following main types can be distinguished according to the manner of development.

Nuclear endosperm

In this type the first divisions are not followed by wall formation, and the nuclei usually take up a parietal position and a large vacuole forms in the centre of the embryo sac. These nuclei may remain free in the cytoplasm of the embryo sac throughout the entire development, or later walls may develop in at least certain parts of the embryo sac, as in *Capsella bursa-pastoris*. Sometimes a few nuclei may divide at a faster rate than the others and so isolated groups or "nodules" are formed. These "nodules" become surrounded by a distinct cytoplasmic membrane (Fig. 190, no. 4; Fig. 197, no. 1). In this type, as in the following types, there are many variations which are discussed in detail by Maheshwari (1950).

Cellular endosperm

In this type the first division of the endosperm nucleus is accompanied by the formation of a wall which is usually horizontal, but which may sometimes be longitudinal or diagonal (Fig. 197, nos. 6–11). The planes of the following divisions may be parallel to that of the first division, but a short while afterwards walls develop in different planes, so that the mature endosperm consists of a tissue the cells of which are orientated in different directions.

In certain plants (e.g. *Thesium Impatiens, Acanthus, Lobelia* and *Lobularia*) *haustoria* of peculiar structure develop at one or both poles of the endosperm (Fig. 198, nos. 1, 2). These haustoria may penetrate deep into the neighbouring tissues of the ovule and from these tissues they transfer nutrients to the developing endosperm. In certain plants secondary haustoria develop laterally from endospermal cells close to the micropyle or chalaza.

Helobial endosperm

This type of endosperm constitutes an intermediate form between the nuclear and cellular types of endosperm. It occurs in different angiosperm genera, e.g. *Asphodelus, Muscari, Ornithogalum, Saxifraga* and *Echium*.

Most typically, endosperm of this type develops in the following manner. The first division of the endosperm nucleus is accompanied by the formation of a horizontal wall which divides the embryo sac into two, usually unequal, chambers of which the micropylar one is large and the chalazal, small (Fig. 197, nos. 2–5). This is followed by several nuclear divisions in

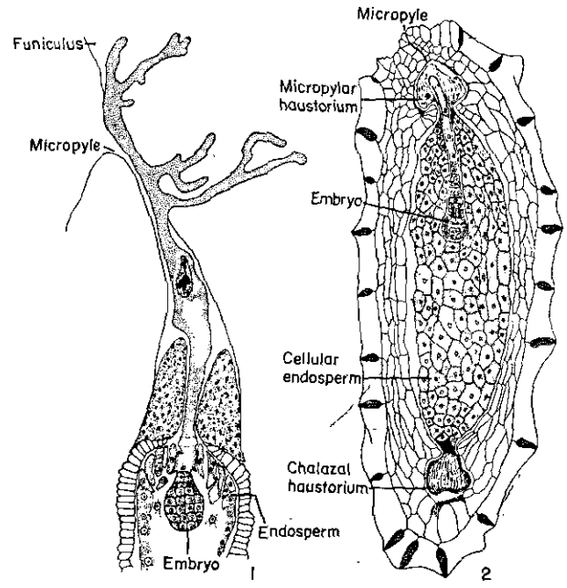


FIG. 198. 1, Upper portion of the ovule of *Impatiens roylei* showing the hypha-like branches of the haustorium which penetrate into the tissue of the funiculus. 2, Longitudinal section of the ovule of *Lobelia amoena* showing the cellular endosperm, and micropylar and chalazal haustoria. (Adapted from Maheshwari, 1950.)

the micropylar chamber where the resulting nuclei remain free, while in the chalazal chamber the nucleus does not divide or undergoes only a few divisions. In the course of further development the amount of cytoplasm in the chalazal chamber is reduced and the nuclei begin to disintegrate. Simultaneously, in many species, cell walls may appear in the micropylar chamber.

No doubt intermediate forms exist between the three above-mentioned endosperm types. It is as yet not clear whether the course of phylogenetic development has been from the nuclear to the cellular type, or vice versa (Maheshwari, 1950).

DEVELOPMENT OF THE EMBRYO

After its formation, the zygote commonly enters a dormant stage for a certain period. At the same time the large vacuole which was still present in the egg cell disappears and the cytoplasm becomes more homogeneous. Usually the zygote begins to divide after the division of the endosperm nucleus. There are plants, e.g. *Oryza* and *Crepis*, in which the zygote begins to divide a few hours after fertilization, while in others the first division takes place only much later. In *Pistacia vera*, for example, the first division takes place about two months after fertilization.

The plane of the first division of the zygote is almost always transverse. As a result of this division two cells are obtained; that closer to the micropyle is termed the *basal cell*, and the other, the *terminal cell*. During the course of further development the terminal cell may divide transversely or longitudinally. The basal cell usually divides transversely. However, in certain genera this cell does not divide but enlarges to form a large, sac-like cell. (Wardlaw, 1955.)

Dicotyledonous embryo

On the basis of the differences in the manner of development of the proembryo to the four-celled stage, dicotyledonous embryos have been classified into five main types (Schnarf, 1929; Johansen, 1945; Maheshwari, 1950).

The terminal cell divides longitudinally

(a) The basal cell does not participate in the formation of the embryo, or it participates to a small extent only... *crucifer type* (Fig. 199, nos. 1–21).

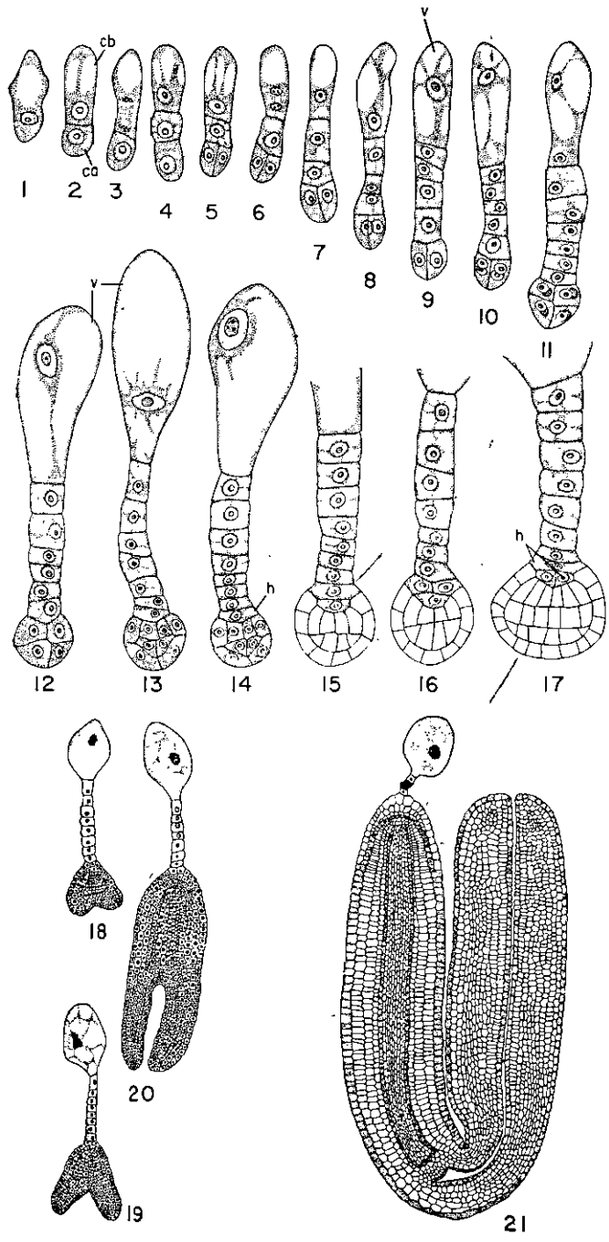
(b) The basal and terminal cells participate in the formation of the embryo... *asterad type* (Fig. 200, nos. 1–6).

The terminal cell divides transversely

(a) The basal cell does not participate in the formation of the embryo or it participates to a small extent only.

(i) The basal cell develops into a *suspensor* which may be two or more cells long... *solanad type* (Fig. 200, nos. 7–14).

FIG. 199. Development of the embryo of *Capsella bursa-pastoris*. Explanation in text. (Adapted from Souèges, 1914, 1919 and Maheshwari, 1950.)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(ii) The basal cell does not divide. If a suspensor is present, it develops from the terminal cell... *caryophyllad type.*

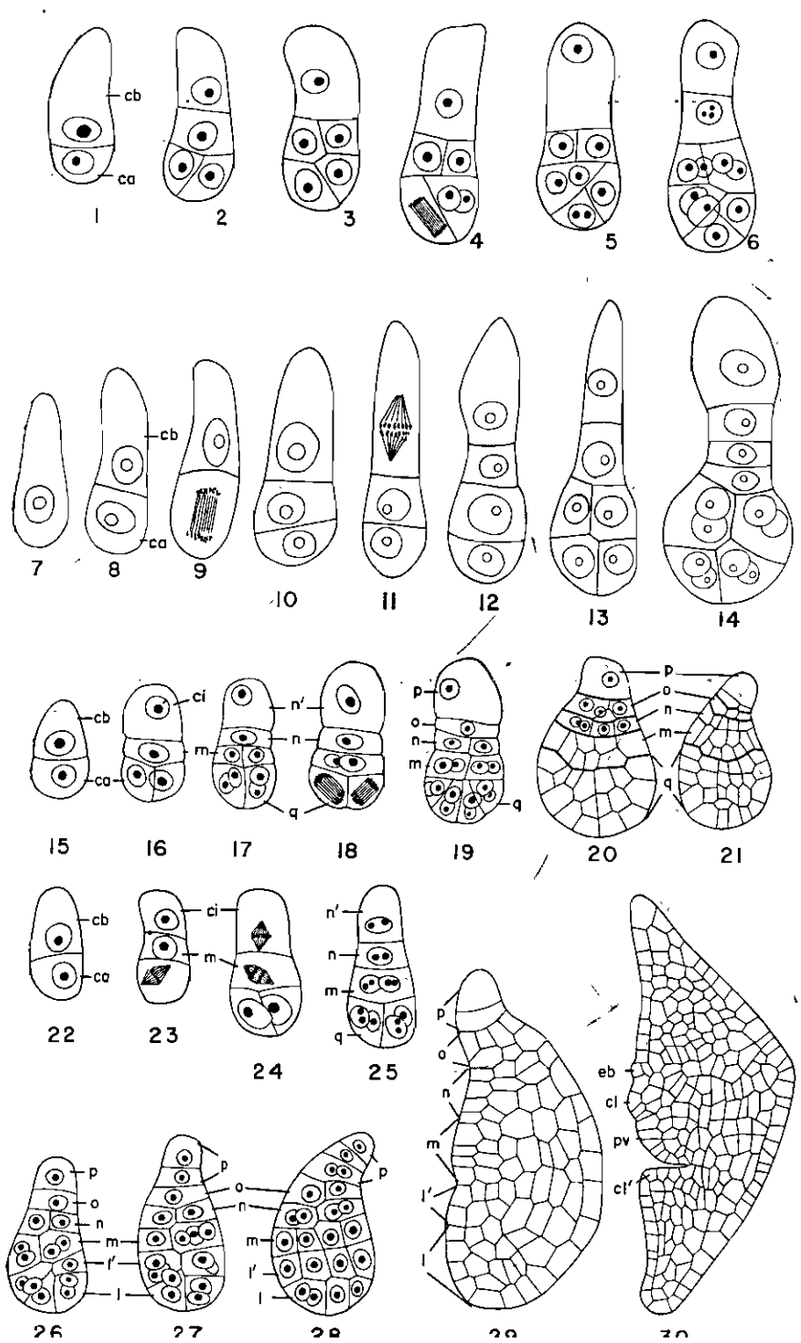
(b) The basal and terminal cells participate in the formation of the embryo... *chenopodiad type.*

Below a detailed description of the embryo development of *Capsella bursa-pastoris* (crucifer type) is given (Fig. 199, nos. 1–21). The embryo of this plant was among the first to be studied (Hanstein, 1870; Souèges, 1914, 1919). In this species the first division of the zygote is transverse to form a basal cell (*cb*) and a terminal cell (*ca*) (Fig. 199, no. 2). The basal cell divides transversely, and the terminal longitudinally (Fig. 199, nos.3–5) to form a four-celled proembryo. Each of the two new terminal cells then divides longitudinally so that the newly formed walls are perpendicular to the first-formed wall. Thus four cells, which are collectively termed the *quadrant*, are formed (Fig. 199, no. 10). The cells of the quadrant then divide transversely to form eight cells—the *octant*—arranged in two tiers (Fig. 199, no. 11; Fig. 190, no. 4). Later each of the octant cells undergoes a periclinal division to form a protodermal and an inner cell (Fig. 199, nos. 13,14). The subsequent divisions of the protodermal cells are anticlinal. The ground meristem and the procambium of the hypocotyl and the cotyledons develop from the inner cells as a result of further division and differentiation (Fig. 199, nos. 15–21).

Together with the development of the embryo proper, the two cells, derived from the division of the basal cell, divide to form a suspensor which consists of a row of six to ten cells (Fig. 199, nos. 2–19). The suspensor cell closest to the micropyle enlarges and becomes sac-like (*v*), and it apparently functions as a haustorium. The suspensor cell closest to the embryo is termed the *hypophysis* (*h*) and it becomes part of the embryo. This cell undergoes transverse and longitudinal divisions to form two four-celled tiers. The root cap and the neighbouring protoderm develop as a result of further divisions of the cells of the tier closest to the row of the suspensor cells, and the second tier contributes cells to the cortex of the radicle.

Meanwhile, the cells of the embryo proper continue to divide, especially in those two areas where the cotyledons will develop. At this stage the embryo is heart-shaped in longitudinal view (Fig. 199, no. 18). Later the hypocotyl and cotyledons elongate as a result of further cell division (Fig.

FIG. 200. 1–6, Development of the embryo of *Geum urbanum* (asterad type). 7–14, Development of the embryo of *Nicotiana* (solanad type). 15–21, Development of the embryo of *Muscari comosum*. 22–30, Development of the embryo of *Poa annua*. Explanations in text. (Adapted from Maheshwari, 1950.)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199, nos. 19, 20). During still later stages of development the cotyledons bend to conform to the shape of the embryo sac (Fig. 199, no. 21).

In some plants, e.g. *Sedum acre*, the sac-like suspensor cell closest to the micropyle may develop a branched haustorium.

Monocotyledonous embryo

There is no important difference in the first divisions of the mono- and dicotyledonous embryos, but in further developmental stages there are distinct differences. In the mature embryo of nearly all dicotyledons (except for a few genera of the Umbelliferae and one species of *Ranunculus)* the shoot apex is found between the bases of the two cotyledons, while in the monocotyledonous embryo the shoot apex is lateral to the single cotyledon.

As examples of the development of monocotyledonous embryos those of *Muscari comosum* (Liliaceae) and *Poa annua* (Graminëae) will be given. In *Muscari comosum* (Fig. 200, nos. 15–21), according to Souèges (1932) and Maheshwari (1950), the basal cell divides transversely, and the terminal cell longitudinally (Fig. 200, no. 16). Following this, the two terminal cells and the cell closest to them (*m*) divide longitudinally, and the cell closest to the micropyle divides transversely into two cells, *n* and *n'* respectively (Fig. 200, no. 17). The cell *n'*, which is now the closest to the micropyle, also divides transversely to form the cells *o* and *p*. After this all the cells, including those of the quadrant (*q*), divide longitudinally or diagonally (Fig. 200, nos. 18, 19). Eventually the cotyledon develops from the tier of cells indicated by *q*, the hypocotyl and shoot tip from *m*, the root initials from *n*, the root cap from *o*, and the suspensor from the cell *p* (Fig. 200, nos. 20, 21).

In *Poa annua* (Fig. 200, nos. 22–30), as described by Souèges (1924) and Maheshwari (1950), the development of the embryo differs from that of *Muscari* principally in the fact that the cells of the quadrant divide transversely to form two tiers *l* and *l'* (Fig. 200, nos. 26, 27), as well as in having differences in the structure of the embryo in the early stages of development (Fig. 200, nos. 29, 30). In *Poa* the *scutellum* and part of the *coleoptile (cl')* develop from the two terminal tiers, *l* and *l'*. The remaining portion of the coleoptile (*cl*), and the shoot and root tips develop from the tier indicated by *m*. The root cap, the *coleorrhiza* and the *epiblast* (*eb*) develop from the tier of cells, *n*. From the remaining cells, *o* and *p*, which are close to the micropyle, the *hypoblast* (termed suspensor in other plants) develops (Fig. 220, no. 2).

Explanations and details of the parts of the mature embryo are given in Chapter 21.

In all mature embryos, no matter what the type of development, differ-

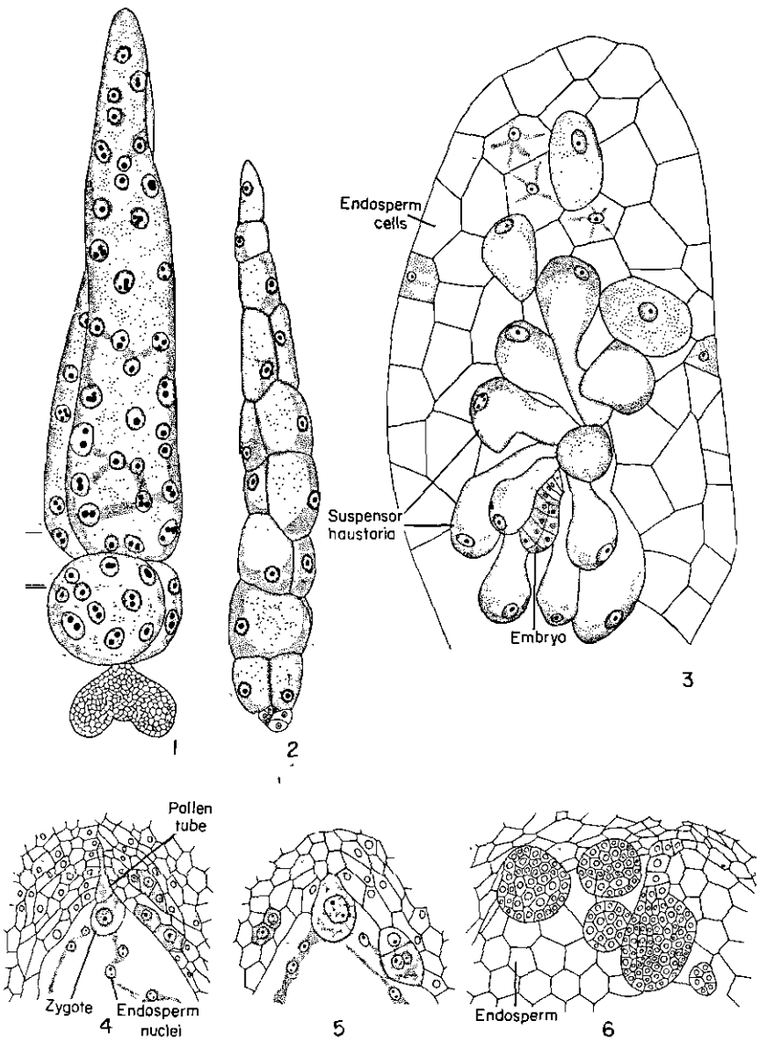

FIG. 201. 1–2, Different types of suspensors in the Papilionaceae. 1, *Orobus angustifolius* in which the suspensor consists of large multinucleate cells. 2, *Cicer arietinum* in which the suspensor consists of two rows of relatively large uninucleate cells. 3, *Asperula* showing young embryo with suspensor haustoria. 4–6, Development of adventitious embryos in *Poncirus trifoliata*. 4, Micropylar portion of the embryo sac showing a fertilized egg cell, pollen tube, endosperm nuclei, and certain nucellar cells (stippled) which are enlarged, rich in cytoplasm and which have large nuclei. 5, As in no. 4, but at a later stage of development. 6, Still later stage, showing numerous embryos in the endosperm. Only the embryo that developed from the zygote has a suspensor. (Adapted from Maheshwari, 1950.)

entiation into root apex, hypocotyl, cotyledon or cotyledons and shoot apex takes place. However, in certain plants. e.g. the Orchidaceae and the Rafflesiaceae, the embryo remains small and oval, and is undifferentiated (Swamy, 1949a).

VARIATION IN STRUCTURE OF THE SUSPENSOR

In most plants the function of the suspensor is only to push the embryo into the endosperm, but in some plants it may develop into a large haustorium which penetrates between the cells of the endosperm, and, to a certain extent, even between the cells of the tissue surrounding the endosperm. In many genera of the Papilionaceae the suspensor is of the latter type (Guignard, 1882). In *Pisum* and *Orobus* for example, the suspensor consists of two pairs of multinucleate cells; the cells of the pair closer to the micropyle are large and very elongated, and those of the second pair are almost spherical (Fig. 201, no. 1). In *Cicer* the suspensor consists of two rows of uninucleate cells (Fig. 201, no. 2). In the Rubiaceae (Lloyd, 1902; Souèges, 1925) the suspensor at first develops as a multicellular thread, and later the cells closest to the micropyle develop lateral projections. These projections penetrate into the endosperm and their tips swell (Fig. 201, no. 3).

APOMIXIS

Apomixis is a process of asexual reproduction in which no nuclear fusion takes place and which occurs in place of sexual reproduction. Maheshwari (1950) distinguished four types of apomixis.

1. *Non-recurrent apomixis.* The megaspore mother cell undergoes the regular meiotic division to form the haploid embryo sac. The new embryo develops from the egg cell, i.e. *haploid parthenogenesis*, or from any other cell of the embryo sac, i.e. *haploid apogamy*. As plants thus formed contain only one set of chromosomes they are usually sterile and so the process is not repeated in the next generation.

2. *Recurrent apomixis.* The embryo sac may develop from a sporogenous cell—*generative apospory*—or from other cells of the nucellus—*somatic apospory*. In this case all the cells are diploid and the embryo may develop from the egg cell (*diploid parthenogenesis*) or from any other cell of the embryo sac (*diploid apogamy*).

3. *Adventive embryony.* The embryo does not develop from the cells of the embryo sac but from a cell of the nucellus or the integuments. This type of development is also known as *sporophytic budding*.

4. *Vegetative reproduction.* In this type of development the flowers, or parts of them, are replaced by bulbils or other vegetative propagules, which may germinate while still on the plant.

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POLYEMBRYONY

The term *polyembryony* refers to the appearance of two or more embryos in a single seed. The processes of apomixis are often accompanied by the formation of a few embryos from the same ovule. Sometimes a normal embryo may develop together with those produced by apomixis. In a single ovule of certain species of *Citrus*, for example, three to twelve apomixial adventitious embryos (Fig. 201, nos. 4–6) may develop alongside the normal embryo (Webber and Batchelor, 1943).

Numerous embryos may develop as a result of the formation of growths on the multicellular body derived from the zygote, which change, during the course of development, into independent embryos. Sometimes additional embryos may be formed by the synergids or the antipodal cells that may be fertilized by male gametes brought into the embryo sac by additional pollen tubes, or even without fertilization. (For more details on polyembryony Maheshwari (1950) should be consulted.)

Pseudo-polyembryony may also result when two or more nucelli, each of which gives rise to a normal embryo, fuse.

In addition to other anatomical characters, the structural and developmental features of embryology have recently been shown to be of great value in the solution of taxonomic problems (Maheshwari, 1950, 1959, 1963; Palser, 1959; Rau, 1962; Subramanyam, 1962). Such embryological features include the type of tapetum, the manner of division of the pollen mother cells, the shape and organization of the pollen grains, the structure of the ovule, the thickness of the nucellus, the development of the megaspore and embryo-sac, the path of entry of the pollen tube into the embryo sac, type and development of the endosperm, and the structure and development of the embryo.

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CHAPTER 20

THE FRUIT

THE fruit generally develops from the gynoecium, but in many fruits other organs also participate. Such organs may be the tepals (*Morus*), the receptacle (*Fragaria*), bracts (*Ananas*), the floral tube, which is formed by the floral organs together with the receptacle (*Pyrus malus*), or the enlarged axis of the inflorescence (*Ficus*). In cases where organs other than the gynoecium participate in the formation of the fruit, the fruit is termed a false fruit or *pseudocarp*.

It is generally accepted that the fruit develops after fertilization, but this is not always so. Fruits of many plants, such as certain varieties of *Musa*, *Citrus* and *Vitis*, develop without the formation of seeds. This phenomenon is termed *parthenocarpy*.

There are different methods of fruit classification (Winkler, 1939, 1940; McLean and Ivimey-Cook, 1956, and others). The fruits are classified into a few types on the basis of two criteria. The main criterion is the degree of hardness of the *pericarp*, i.e. the fruit wall, — whether it is dry and hard or soft and fleshy or juicy. The second criterion is the ability of the fruit to dehisce or not when ripe.

Dry fruits

DEHISCENT FRUITS

(a) Fruits that develop from a single carpel.

(i) *Follicle*: a pod-like fruit which generally splits down the ventral side (*Delphinium*, *Brachychiton*).

(ii) *Legume*: a fruit that splits into two valves along a suture which surrounds the fruit (Leguminosae).

(b) Syncarpous fruits, i.e. those developing from an ovary with two or more carpels.

(i) *Siliqua*: a pod-like fruit consisting of two carpels which is considered by many to be a special type of capsule (see below). The suture between the carpels' margins forms a thick rib, termed *replum*, around the fruit. From these sutures, which bear the

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SCHIZOCARPIC FRUITS

Schizocarpic fruits are those that develop from multiloculate ovaries that separate when ripe into akenes, the number of which is equal to the number of carpels. Such a fruit is termed a *schizocarp* and each of the parts into which it separates are termed *mericarps* (e.g. many genera of the Malvaceae such as *Malva* and *Lavatera*).

The *cremocarp* of the Umbelliferae is also a schizocarp, but it is actually a false fruit as it develops from an inferior ovary. In the Labiatae the fruit also separates into akene-like mericarps (*nutlet* or *coccus*) each of which consists of half a carpel enclosing a single seed.

From a phylogenetic view point the follicle, which develops from an apocarpous gynoecium, is considered the most primitive type of fruit.

Fleshy fruits

Berry or *bacca*. A fruit in which the pericarp is usually thick and juicy and in which three strata can be distinguished: the outer stratum which usually contains the pigment of the fruit—*exocarp;* the relatively thick stratum below it—*mesocarp;* and the membranous inner stratum—*endocarp*. This fleshy pericarp may enclose one or many seeds (e.g. grape, tomato). The fruit of *Citrus*, which is also a berry, has been specially termed an *hesperidium*. The fruits of *Coffea*, *Sambucus*, *Hedera*, *Cucumis* and *Musa* are also berries but, theoretically, they are false fruits as they develop from inferior ovaries; they differ from typical false fruits in that the extra-carpellary parts contribute only a small part in the construction of their pericarp.

Drupe. This fruit differs from the berry in that the endocarp is thick and hard (*Prunus*, *Mangifera*, *Pistacia*, *Juglans*). The "nut" of *Cocos* is a drupe in which the mesocarp consists of fibrous matter.

Aggregate fruits are obtained when the carpels of an apocarpous gynoecium ripen individually but in the course of ripening the individual fruits of a flower aggregate to form a single unit, as, for example, in *Rubus*.

Histological structure of the pericarp

There is no distinct tissue differentiation in the pericarp prior to the ripening of the fruit. During the development of the fruit the number of cells increases and the parenchymatous ground tissue may remain as it is, or part of it may become sclerenchymatous. In the mature fruit the above three layers—the exocarp, mesocarp and endocarp—can be distinguished but sometimes only the exo- and endocarps are discernible. However in

placentae on their inner surfaces, two membranes grow inwards where they fuse to form a false septum which divides the locule into two. When the fruit ripens the two valves separate from the replum to which the seeds remain attached and which itself remains as a frame around the septum. Such fruits occur in most genera of the Cruciferae.

(ii) *Capsule*: a fruit developing from two or more carpels and dehiscing in different ways that are of taxonomic importance. Usually the split is from apex down and then it may be along the dorsal bundle of each carpel and the dehiscence is said to be *loculicidal* (e.g. *Epilobium, Iris*), or between the carpels and the dehiscence is said to be *septicidal* (e.g. *Hypericum*). If the outer wall of the fruit breaks away from the septa, which remain attached to the axis, the dehiscence is said to be *septifragal.* In some species of *Campanula* and *Papaver*, the dehiscence is *porous*, i.e. by means of small pores which develop in the pericarp. In *Anagallis* and *Hyoscyamus*, the dehiscence is *circumscissile*, i.e. by means of a transverse split which results in the formation of a lid. When the dehiscence is by means of outwardly flared teeth, it is said to be *valvate*. In all the examples given above, the portions into which the fruit splits are termed *valves*.

INDEHISCENT DRY FRUITS

(a) *Achenium, achene* or *akene*: a single-seeded fruit formed by one carpel (*Ranunculus*).

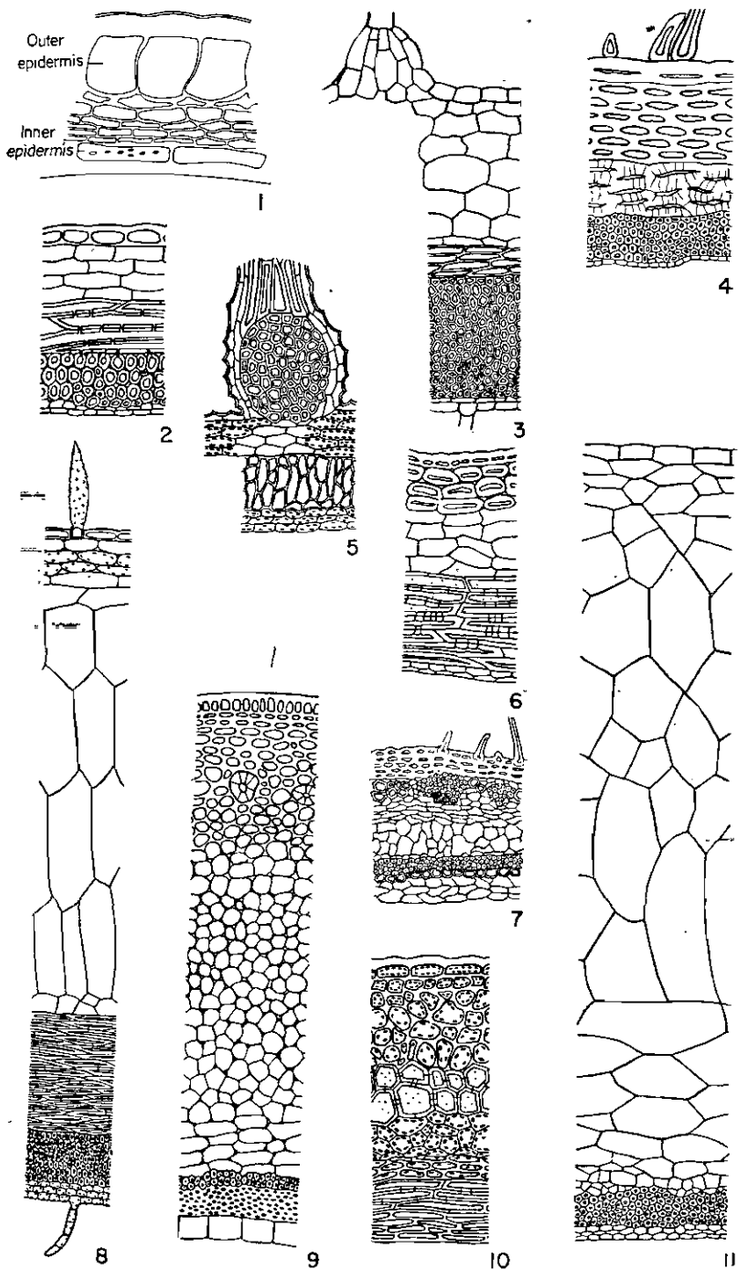
(b) *Cypsela*: a single-seeded fruit developing from an inferior ovary and thus surrounded by other floral tissues in addition to the ovary wall (Compositae). This is actually a false fruit.

(c) *Nux* or *nut*: a single-seeded fruit that develops from an ovary that originally consists of a few carpels of which all but one, in which a single ovule develops, degenerate (*Valerianella* and *Tilia*). The acorn of *Quercus* together with its involucre is a false nut as it develops from an inferior ovary.

(d) *Caryopsis*: a one-seeded fruit in which the seed wall is adnated to the pericarp (Gramineae)

(e) *Samara*: a winged one-seeded fruit (*Ulmus* and *Fraxinus*).

There are also indehiscent dry fruits consisting of several carpels and containing one or more seeds, i.e. *carcerulus* (in a few Cruciferae, as, for example, *Crambe*).


Outer epidermis
Inner epidermis
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many fruits the exo- and endocarps may consist only of epidermal tissues and the pericarp then consists mainly of mesocarp. The division into these pericarp layers is only one of convenience to facilitate the anatomical description of mature fruits and these layers do not represent separate tissues from the point of view of their origin. In this book this division will also be used in the description of false fruits.

In large fruits vascular bundles, which develop in the ground tissue, are added to the vascular system of the gynoecium (as described in the previous chapter) so that the supply of water and other substances to all parts of the fruit is made possible.

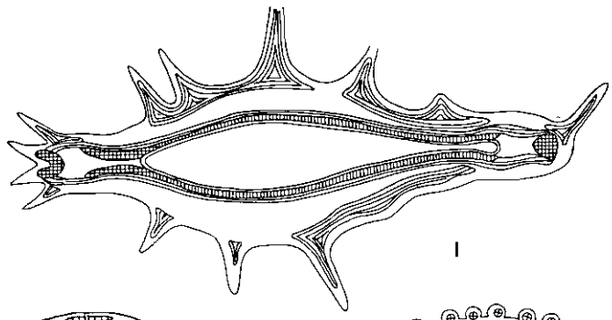
Usually there is a relationship between the manner of fruit and seed dispersal, and the histological structure of the pericarp.

PERICARP OF DRY FRUITS

Dehiscent fruits

Follicle. In the follicle of *Delphinium*, for example, the exocarp (outer epidermis and sometimes also a hypodermal layer) consists of thick-walled cells, the mesocarp is parenchymatous and the endocarp (the inner epidermis) consists of thick-walled cells (Fig. 202, no. 1). The vascular bundles have sclerenchymatous sheaths. The pericarp dries out with the maturation of the fruit and the dehiscence of the follicle, along the line of marginal fusion of the carpel, results from this drying process.

Legume. The following is a description of the basic structure of a legume of the Leguminosae. The exocarp usually consists of epidermis only, the mesocarp—of relatively thick parenchyma, the endocarp—of sclerechyma on the inside of which is usually a thin-walled epidermis or a few parenchyma layers and an epidermis. The vascular bundles are situated in the parenchyma of the mesocarp and they are accompanied by sclerenchyma. Although the general structure of the legume in most species of the Leguminosae is uniform, there may be differences in the relative thickness of the different pericarp tissues, the structure of their cells, the orientation of the different elements and, sometimes, also in the submicroscopic structure (Monsi, 1943; Fahn and Zohary, 1955). Thus in *Astragalus macrocarpus*, the outer epidermal cells are thin walled (Fig. 202, no. 11), while in *Lupinus hirsutus* (Fig. 202, no. 6) and species of *Vicia* they are thick walled. The epidermis may be typically uniseriate or a hypodermis may be present, as, for example, in *Lupinus hirsutus*. The tissue of the mesocarp may not always be parenchymatous and in certain legumes it is entirely collenchymatous (*Calycotome villosa*, Fig. 202, no. 4) or it may be partly collenchymatous and partly parenchymatous (*Retama raetam*, Fig. 202, no. 9). In some legumes there are sclereids scattered in the collenchyma



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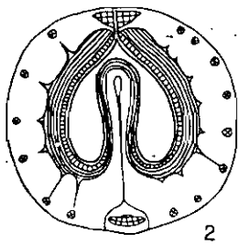

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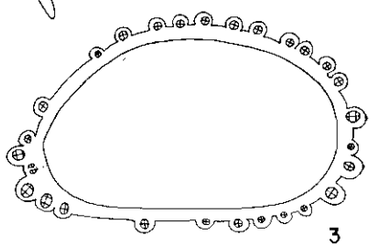

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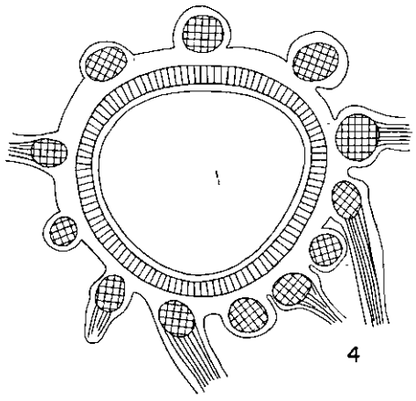

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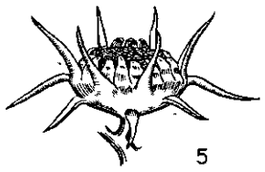

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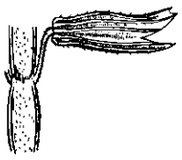

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10

(*R. raetam* and *Anagyris foetida*, Fig. 202, nos. 9, 10). The sclerenchyma, which constitutes most of the endocarp, consists either of one zone of fibres which are all arranged in one direction (*Astragalus macrocarpus*, Fig. 202, no. 11; *Acacia raddiana*, Fig. 202, no. 7; *Lupinus hirsutus*, Fig. 202, no. 6) or of two zones in which the longitudinal orientation of their cells differs (*Astragalus hamosus*, Fig. 202, no. 2; *Hymenocarpos circinnatus*). In the legumes of certain species there is no sclerenchymatous region at all (*Glycyrrhiza echinata; Trifolium subterraneum; Melilotus*, Fig. 203, no. 3). In some species the sclerenchymatous stratum of the endocarp is lined on the inside not by parenchyma but by collenchyma (*Retama raetam*, Fig. 202, no. 9; *Anagyris foetida*, Fig. 202, no. 10). The cell walls of the inner epidermis are usually thin, but in the legumes of certain species they may be slightly thickened (*Trifolium stellatum*) or the cells may be fibre-like (*Trigonella arabica*). Spines, which usually consist of sclerenchyma, develop on certain legumes (*Scorpiurus muricata*, Fig. 203, no. 4; *Hedysarum pallens*, Fig. 203, no. 1).

The two valves of a dried legume usually twist (Fig. 210, no. 2). This is brought about by the anisotropic shrinkage of the thickened walls of the pericarp cells. This feature is a result of the orientation of the microfibrils and cellulose crystals in the walls. The greatest swelling of the cell walls takes place in the direction at right-angles to the longitudinal axis of the microfibrils. Because of this the greatest shrinkage, during the drying out of the valves, is also in this direction. In *Vicia* and in many species of other genera (Fahn and Zohary, 1955) the sclerenchyma cells of the endocarp are orientated at an angle of about 45° to the longitudinal axis of the legume, while the elongated, thick-walled epidermal or epidermal and hypodermal cells are orientated in a similar angle but in the opposite direction. In the valves of these legumes the microfibrillar orientation relative to the cell axis is the same in both the endo- and exocarp, but as the cell axes in these two strata of the pericarp are, themselves, differently orientated, tension develops during the drying out of the valves. This tension results in the twisting of the valves after the forces that keep the cells together in the mature abscission zone are overcome. The legume then dehisces explosively, the valves contort and the seeds are expelled.

FIG. 202. 1, Portions of a cross-section of the follicle wall of *Delphinium*. 2–11, Portions of sections of the walls of legumes of different species of the Leguminosae. 2, *Astragalus hamosus*, cross-section. 3, *A. amalecitanus*, cross-section. 4, *Calycotome villosa*, oblique section. 5, *Scorpiurus muricata*, cross-section. 6, *Lupinus hirsutus*, oblique section. 7, *Acacia raddiana*, cross-section. 8, *Astragalus fruticosus*, cross-section. 9, *Retama raetam*, oblique section. 10, *Anagyris foetida*, oblique section. 11, *Astragalus macrocarpus*, oblique section. In all the diagrams the outer epidermis is uppermost.

termine the direction of the bending of the teeth or valves. The thinner walls of the epidermis, or of the sclerenchymatous tissue below the epidermis, or of the sclerenchyma accompanying the vascular bundles, usually

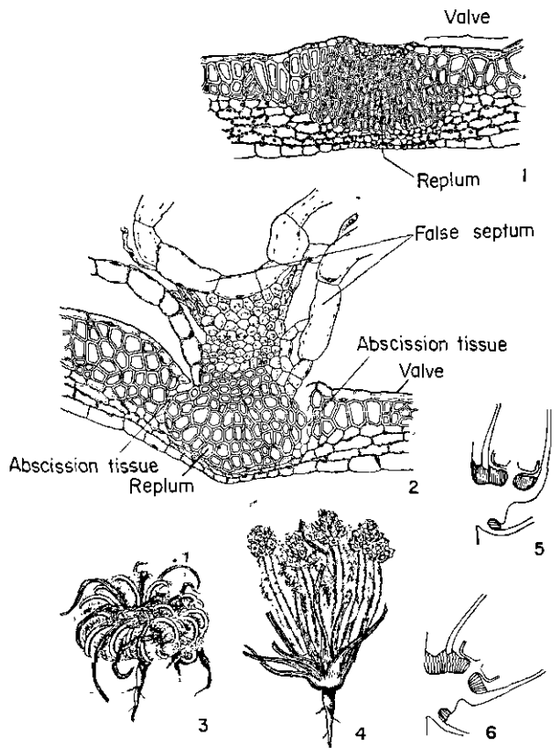


FIG. 204. 1 and 2, Cross-sections of both types of fruits of *Aethionema carneum* showing the region around the replum. 1, Of a young indehiscent siliqua. 2, Of a young dehiscent siliqua. 3–6, *Plantago cretica*. 3, Entire plant in dry condition. 4, As in no. 3, moist. 5 and 6, Diagrams of longitudinal sections through the remnants of a flower and its bracts which remain on the plant even after the ripening of the fruit. Cohesion tissue, represented by hatching. 5, Dry, showing the cohesion tissue, to be contracted. 6, Moist, showing the expansion of the cohesion tissue which causes the sepals and bracts to spread.

constitute the resistance tissues. The swelling and, therefore, the shrinkage of these tissues along the axis of bending is relatively small. These differences in swelling and shrinkage cause the characteristic opening movements. In capsules abscission tissue is developed between the teeth or valves. In capsules that open by means of a lid, e.g. the fruits of *Hyoscyamus, Plantago, Anagallis* and *Portulaca*, the abscission tissue develops as a ring around the capsule.

There are many variations in the structure connected with the opening mechanism that has been described above. In the legumes of *Wisteria sinensis* (Monsi, 1943) and *Lupinus angustifolius* (Fahn and Zohary, 1955), for example, all the sclerenchymatous cells of the endocarp have uniform orientation, but two zones, in which the orientation of the cellulose crystals differ, can be distinguished. These zones, therefore, also differ in the direction of greatest swelling. There are also legumes in which the endocarp sclerenchyma consists of two layers that are distinguished by cell orientation (*Astragalus fruticosus*, Fig. 202, no. 8; *A. hamosus*, Fig. 202, no. 2; *Hedysarum pallens*, Fig. 203, no. 1). In the legumes of other species, e.g. *Ornithopus compressus*, the endocarp sclerenchyma consists of two zones, as mentioned above, but in one zone the orientation of the fibrils is parallel to the longitudinal cell axis and in the second zone, at right-angles to it. As a result of this the fibrillar orientation, relative to the axis of the legume, is the same in the two zones. In these plants, in addition, the orientation of the fibrils of the epidermal cells is parallel to that of the fibrils in the sclerenchyma and therefore the fruit does not dehisce when dry. Abscission tissue is also not developed in such legumes.

Siliqua. In the pericarp of the siliqua the cells of the exo- and mesocarp are usually thin walled and the endocarp tissue is sclerenchymatous. An abscission zone usually develops between the replum and the valves (Fig. 204, no. 2).

Capsule. The epidermal cells of many capsules, which open by teeth or valves, have very thick outer walls while the mesocarp tissue is parenchymatous. Elongated, thick-walled cells may sometimes be present below the epidermis (Fig. 205, no. 1). The inner epidermal cells may also be thick walled. In the capsules of certain species of the Primulaceae, such as *Lysimachia mauritiana*, the cells of the inner epidermis have particularly thick walls on the side closest to the mesocarp (Guttenberg, 1926). The dehiscence of the capsule is also brought about by the anisotropic swelling of the cell walls. The walls that bring about the dehiscence in this case are mainly the very thick walls of the outer or inner epidermis, and it is they that de-

FIG. 203. 1–4, Diagrams of cross-sections of legumes of different species of the Leguminosae. In those places where the sclerenchyma cells are seen in longitudinal section, the sclerenchyma is indicated by parallel lines, and in those places where the cells are cross-sectioned, it is indicated by cross-hatching. 1, *Hedysarum pallens*. 2, *Astragalus fruticosus*. 3, *Melilotus* sp. 4, *Scorpiurus muricata*. 5–10, Hygroscopic movements. 5 and 6, Capitula of *Anvillea garcini*, showing the movement of the involucre bracts. 5, Dry. 6, Moist. 7 and 8, *Salvia horminum*, showing the movement of the pedicel and the mericarp-containing calyx. 7, Dry, showing the pedicel bent downwards bringing the calyx close to the axis of the inflorescence. 8, Moist. 9 and 10, *Cichorium pumilum*, capitula showing movement of the involucre. 9, Dry. 10, Moist.

In the dispersal of the seeds of dry fruits, sepals and extrafloral organs may sometimes participate, e.g. the bracts of the capitulum (*Cichorium*, Fig. 203, nos. 9, 10; *Anvillea*, Fig. 203, nos. 5, 6), floral pedicels (*Salvia horminum*, Fig. 203, nos. 7, 8), axes of inflorescences (*Plantago cretica*, Fig. 204, nos. 3, 4), and entire branches (*Anastatica hierochuntica*) (Steinbrinck and Schinz, 1908; Zohary and Fahn, 1941; Fahn, 1947). The mechanisms of dispersal in these cases are also usually based on the differences in direction of excessive swelling in the different zones of the sclerenchymatous tissues. This *swelling mechanism* also causes the twisting of the "beak" of the mericarp of *Erodium* (Fig. 210, no. 1).

In addition to the swelling mechanism there is the *cohesion mechanism* that is responsible for the movement of organs connected with the dispersal of fruits and seeds. Cohesion tissue occurs, for example, on the outer side of the bracts of many of the Compositae (*Senecio*, *Tragopogon* and *Geropogon*, Fig. 205, nos. 2, 3), between the bases of the rays of the umbel, e.g. *Ammi visnaga* (Fig. 205, nos. 4–6), between the tepals, e.g. *Plantago cretica* (Fig. 204, nos. 5, 6), etc. The cells of cohesion tissues are usually elongated and thin walled; the longitudinal axis of these cells is at right-angles to that of the shrinkage axis of the tissue. As a result of the loss of water the cell walls fold or wrinkle, the cell volume is reduced and the tissue, in shrinking, draws with it the organ that is attached to it. If water is again absorbed by the cells, they swell and the volume of the tissue increases (Guttenberg, 1926; Zohary and Fahn, 1941).

Indehiscent fruits

The histological structure of only three dry indehiscent fruits – cypsela, caryopsis and cremocarp – will be given here.

Cypsela: The anatomical structure and development of the pericarp of *Lactuca sativa* have been described by Borthwick and Robbins (1928). The nucellus almost completely disappears already prior to pollination and the integument is very thick – from eight to twelve cells in thickness. The pericarp increases in thickness, and its cells are similar to, but smaller, than those of the integument. A distinct outer epidermis is discernible in the pericarp. With the maturation of the flower, lysigenous cavities begin to form in the inner portion of the pericarp (Fig. 206, no. 1). During the process of fruit ripening the inner layers of the pericarp disintegrate. About a week after fertilization, with the growth of the embryo and the development of the endosperm, further disintegration of the pericarp tissues, and also of those of the integument, takes place (Fig. 206, no. 2). About 10 days after fertilization the cells of the inner epidermis of the integument disintegrate and their inner walls may adhere to the endosperm where they form a membrane which, in certain fruits, is suberized. This mem-

The rupture between the lid and the rest of the capsule, along this abscission line, is apparently brought about by the fact that the maturing pericarp

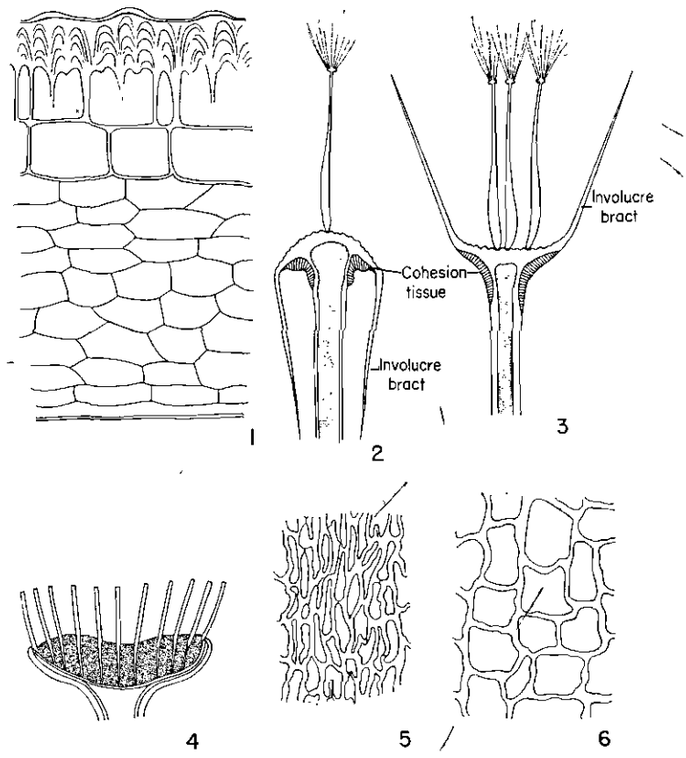


FIG. 205. 1, *Vaccaria pyramidata*, longitudinal section through a tooth of the capsule. The outer epidermis (directed upwards) has very thick walls in which the lamellae are orientated almost perpendicularly to the surface of the teeth. These walls, when wet, are capable of extensive swelling in a longitudinal direction, and the elongated cells below this epidermis and the cells of the inner epidermis, itself, form a tissue that resists this movement. As a result the valves open outwards when they are dry and close when they are moist. 2 and 3, *Geropogon*, showing action of cohesion tissue — hatched areas. 2, Ripe capitulum in dry condition. 3, In moist condition showing that the cohesion tissue, when saturated with water, raises the involucre bracts. 4–6, *Ammi visnaga* 4, Diagram of a cross-section through the base of the compound umbel, showing the bases of the partial umbels to be embedded in coheson tissue (stippled). 5 and 6, Tangential sections through the cohesion tissue. 5, Dry. 6, Moist. (Nos. 4–6, adapted from Guttenberg, 1926.)

dries out and shrinks while the volume of the seeds, which fill the entire cavity of the fruit, does not change (Rethke, 1946; Subramanyam and Raju, 1953).

3). The integumental cells of the mature seed are compressed and partly obliterated, but the outer epidermis may remain as a layer of thick-walled cells.

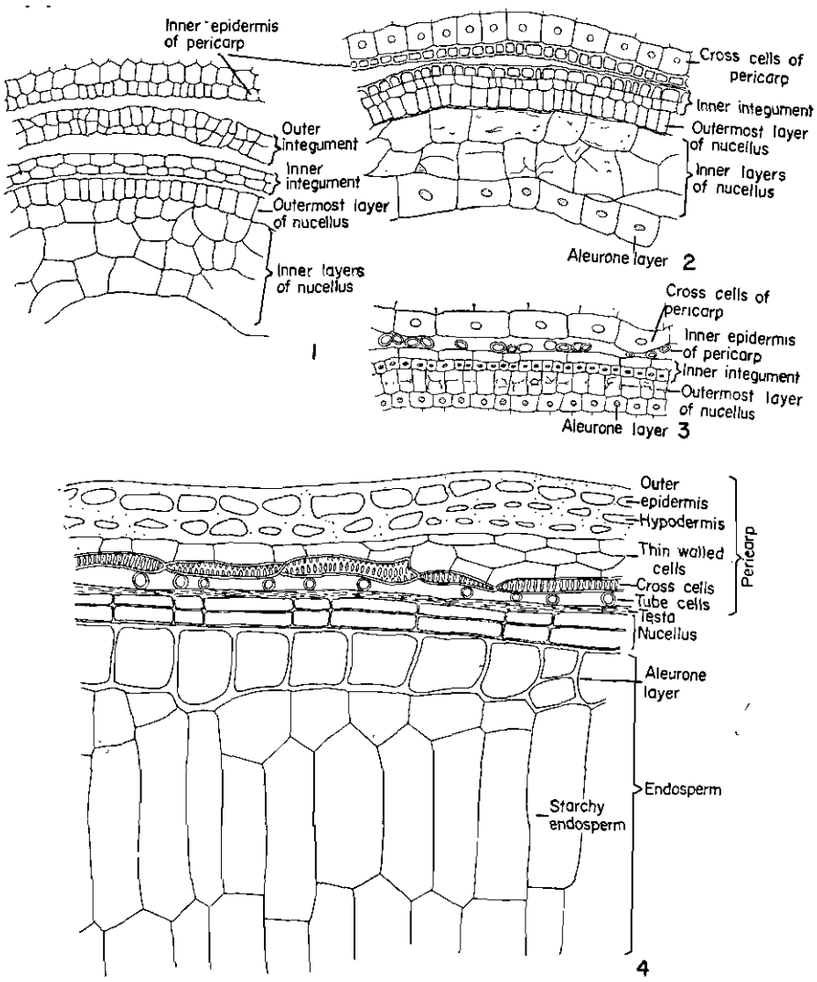


FIG. 207. 1–4, Portions of cross-section through the pericarp of the caryopsis of *Triticum* at different stages of development. (Adapted from Hayward, 1938.)

Caryopsis. The pericarp and the remains of the integuments of the single seed of the caryopsis are completely fused (Krauss, 1933; Bradbury, MacMasters and Cull, 1956). In the caryopsis of *Triticum* (Fig. 207, no.

brane is considered by Borthwick and Robbins to be semipermeable. With the ripening of the cypsela, pericarp ribs which consist of sclerenchymatous tissue become obvious (Fig. 206, nos. 2–4). In the mature fruit the

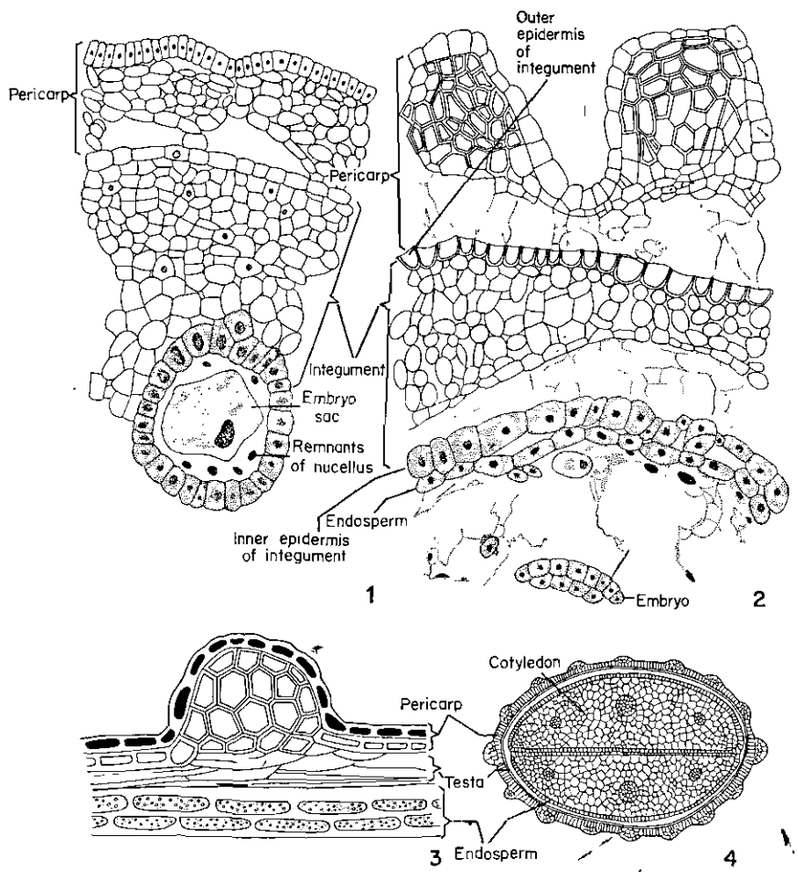


FIG. 206. Development of the pericarp in *Lactuca sativa*. 1, Portion of a cross-section of an ovary 2 hr after fertilization. 2, Portion of a cross-section of the cypsela about a week after fertilization. 3, Mature pericarp. 4, Diagram of a cross-section of an entire cypsela. (Adapted from Borthwick and Robbins, 1928 and Hayward, 1938.)

rest of the pericarp, apart from the ribs, consists of one or two cell layers as a result of the disintegration of the parenchyma cells. Cypselae differ greatly in colour. These differences are partly due to the presence or absence of pigment in the outer epidermal cells of the pericarp (Fig. 206, no.

The maturing mericarps, each of which develops from a single carpel together with a small amount of tissue outside it (inferior ovary), separate one from the other along the area of adnation between them, but they

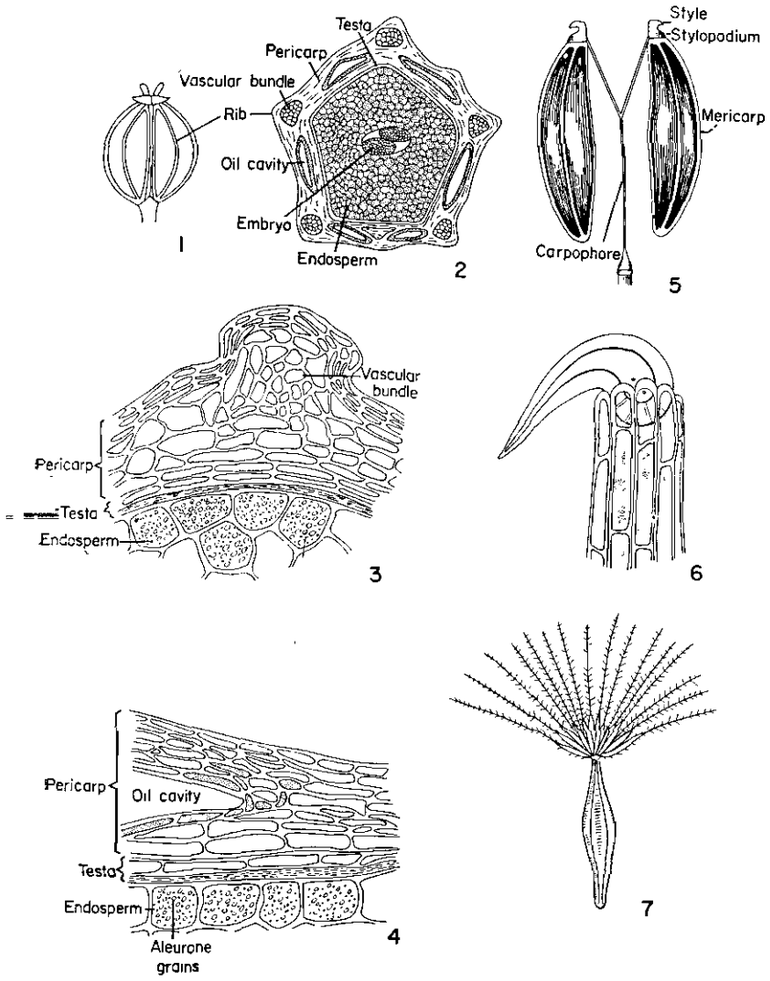


FIG. 208. 1–4, Fruit of *Apium graveolens*. 1, Drawing of the entire cremocarp. 2, Cross-section of a single mericarp. 3, Portion of a cross-section of a mericarp showing the structure of a rib. 4, As in No. 3, in the region of an oil cavity. 5, A mature cremocarp with separated mericarps. 6, Distal portion of spine of the nutlet of *Ranunculus arvensis* showing the pointed, curved cell at its apex by which it becomes attached to the dispersal agents. 7, Cypsela of the Compositae showing the feathery pappus. (Nos. 1–4, adapted from Hayward, 1938.)

4; Fig. 220, nos. 1, 2), for example, three main parts can be distinguished: (1) the caryopsis coat which includes the pericarp, the seed coat and the nucellus; (2) the endosperm; (3) the embryo. Five layers can be distinguished in the pericarp: the outer epidermis, the hypodermis, a zone of thin-walled cells, *cross cells* and *tube cells*. The outer epidermis and the hypodermis together form the exocarp. The cells of the exocarp are elongated in a direction parallel to the longitudinal axis of the caryopsis, and they become compressed and their walls thicken considerably so that, when the caryopsis is ripe, cell lumina cannot easily be distinguished in them. The cross cells are found below the parenchymatous layer and they have thick walls with pits which are elongated transversly to the cell. The longitudinal axis of these cells is at right-angles to that of the exocarp cells. The tube cells constitute the inner epidermis of the pericarp and they occur on the inside of the cross cells. There are large intercellular spaces between the tube cells, the walls of which are pitted and thinner than those of the cross cells. The longitudinal axis of the tube cells is parallel to that of the exocarp cells. The tube cells are only clearly visible on certain parts of the caryopsis (Bradbury *et al.*, 1956). The seed coat, which is adnated to the pericarp, is crushed in the mature caryopsis and therefore it is difficult to discern cells in this zone. When fully mature the seed coat consists only of the inner integument, the outer being completely destroyed. In a section of the caryposis stained with Sudan IV two cuticles are discernible: an outer thick one of the single remaining integument, and a thin one which constitutes that of the nucellus together with that of the inner side of the integument. The nucellus tissue may be partially or entirely digested during the development of the caryopsis. In those parts where nucellus is still present it is discernible as one or two layers of thin-walled cells between the aleurone layer and the seed coat. In the mature caryopsis these nucellar cells are usually crushed and they appear as a thin, glassy zone, which is bright and colourless (Fig. 207, nos. 1–4).

Cremocarp. The fruit of *Apium graveolens* is described here as an example of a cremocarp (Hayward, 1938). Each mericarp has five ribs in which the vascular bundles, accompanied by sclerenchyma, are situated (Fig. 208, nos. 1–3). Between the ribs one to three oil ducts may be present (Fig. 208, nos. 2, 4). The exocarp cells (i.e. the outer epidermis) are small and isodiametric. In surface view they appear lobed. The mesocarp is parenchymatous and its cells have small papillae and finely striated walls. The oil ducts in the mesocarp are surrounded by polyhedral cells which become brown as the fruit ripens. The slightly elongated cells of the innermost layer of the mesocarp are wider than those of the endocarp. The endocarp (the inner epidermis) consists of narrow cells of which the longitudinal axis is parallel to the transverse axis of the mericarp (Fig. 208, nos. 3, 4), or their arrangement is mosaic. Inside the pericarp is the thin seed coat which surrounds the endosperm in which the embryo is completely enclosed.

The dispersal of indehiscent, dry fruits and their seeds is brought about in various ways, and here also a correlation can be found between the manner of dispersal and the anatomical structure of the pericarp. Thus, for instance, on the akenes of *Ranunculus arvensis* strong, hook-like hairs, which consist of extremely thick-walled cells (Fig. 208, no. 6), develop; these hairs enable the fruit to cling to the coats of animals. Cypselae of many of the Compositae develop a characteristic pappus of hairs or bristles which may be branched (Fig. 208, no. 7). The outer cypselae of *Calendula officinalis* are boat-shaped and the margins are widened to form backwardly directed wings. In a cross section of such a cypsela (Fig. 209, no. 1), it is possible to see that the endocarp consists of a thick sclerenchymatous tissue. The centre of the keel, the wings and the ribs on the side opposite the keel consist of large parenchyma cells whose pitted walls are slightly thickened. Most of the region between the epidermis and the inner tissues of the cypsela consists of very long palisade-like cells which have large intercellular spaces between them (Fig. 209, no. 2). This tissue together with the thick-walled large parenchyma cells, which are filled with air, aid in the dispersal of these cypselae by wind.

An outgrowth of large oil-storing cells occurs on the basal part of the fruit of some plants, e.g. *Hepatica triloba*, *Ranunculus ficaria*, *Anemone nemorosa*, *Adonis vernalis* and *Fumaria officinalis*. Such growths are termed *elaiosomes* and they may also occur on seeds (see following chapter). In *Borago officinalis*, *Anchusa* spp., *Ajuga* spp. and other species the elaiosome of the fruit or the mericarp develops from a portion of the pedicel (Schoenichen, 1924). Elaiosomes are thought to be an adaptation to fruit and seed dispersal by ants.

There are many other modifications in the histological structure of dry fruits which are adapted to dispersal by air, water and animals, but it is not within the scope of this book to discuss all of them.

PERICARP OF FLESHY FRUITS

Berry. In a berry all of the ground tissue of the ovary wall develops into a fleshy or juicy tissue, and sometimes other organs may also contribute to the formation of this tissue. In *Lycopersicon*, for example, the greater part of the juicy tissue develops from the placenta. In certain berries the locules of the fruit become filled with growths of the pericarp and placenta (*Physalis*) or of the septa (*Bryonia dioica*) (Kraus, 1949). Below, the structure and development of some special fruits which are considered to be berries, in the wide sense of the term, are described.

Lycopersicon esculentum. This fruit consists of a pericarp and placental tissue on which the seeds are borne. The exocarp consists of an epidermis and three or four layers of collenchyma cells. The epidermal cells are

remain attached to the branched *carpophore* (Fig. 208, no. 5). There are different opinions as to the origin of the carpophore—there are investigators who believe that it arises from the floral axis, while others believe that it develops from the carpels. Jackson (1933) claims that usually only

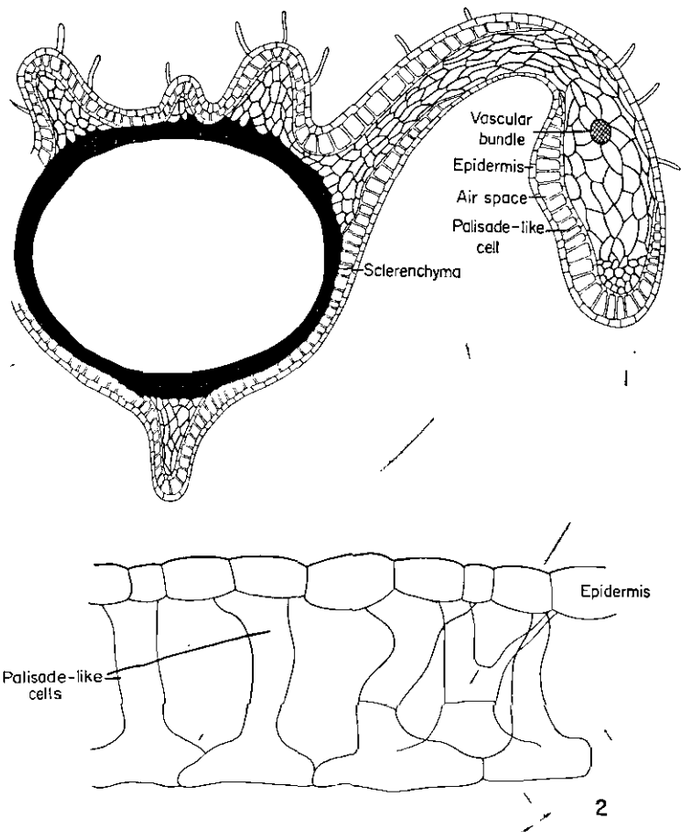
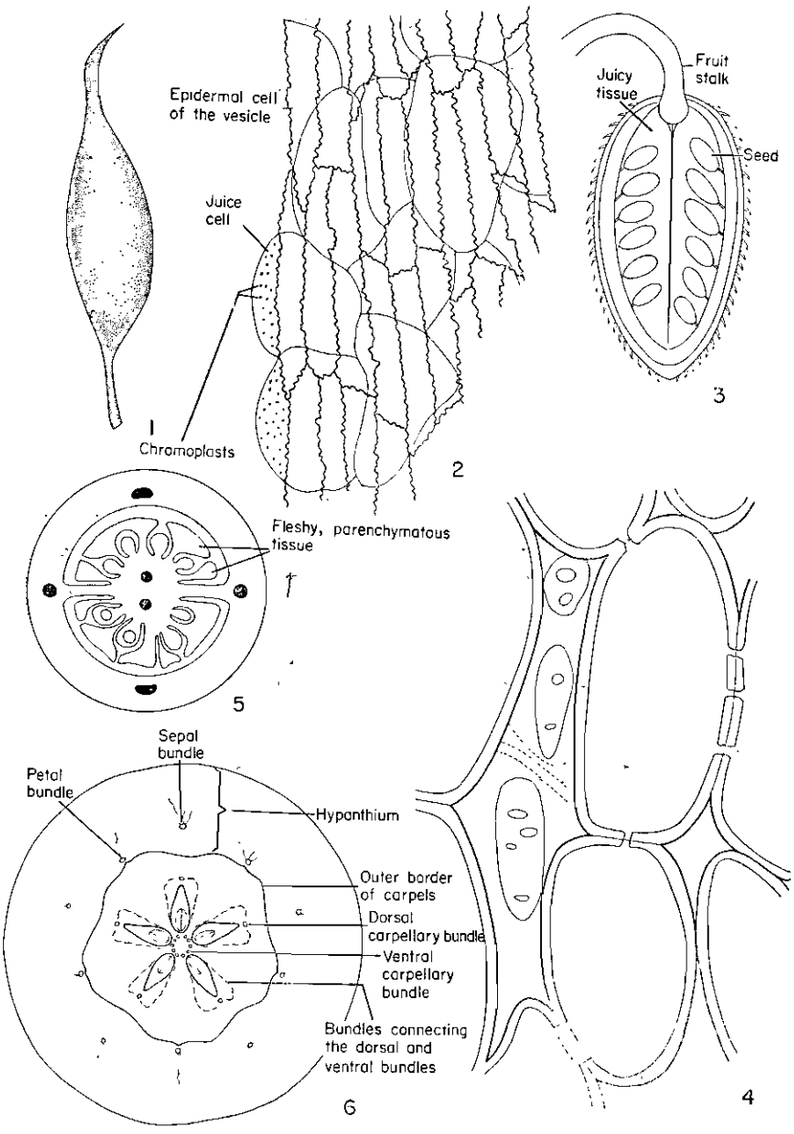


FIG. 209. *Calendula officinalis*. 1, Diagram of a cross-section of the cypsela. 2, Epidermal cells and palisade-like cells, between which there are large air spaces, greatly enlarged. (Adapted from Schoenichen, 1924.)

the basal portion is of receptacular origin while the greater portion of the carpophore is carpellary and contains the ventral carpel bundles. The abscission zone occurs partly between the two mericarps and partly between the mericarps and the carpophore. With the maturation of the cremocarp, an abscission zone also appears within the carpophore, in the lignified tissue between the two ventral veins. This abscission zone splits the carpophore into two.


Epidermal cell of the vesicle
Juice cell
Chromoplasts
1
2
Juicy tissue
Fruit stalk
Seed
3
Fleshy, parenchymatous tissue
5
Sepal bundle
Petal bundle
Hypanthium
Outer border of carpels
Dorsal carpellary bundle
Ventral carpellary bundle
Bundles connecting the dorsal and ventral bundles
6
4

polyhedral and are covered by a thin cuticle. The number of epidermal cells does not increase greatly with the development and growth of the fruit, and so the epidermal cells of the mature fruit are much larger than

FIG. 210. 1, *Erodium*, photograph of a mature mericarp in a dry condition. 2, *Spartium junceum*, photograph of mature legumes which have dehicsed as a result of the twisting of the valves. (Photographs, courtesy of D. Koller.)

those in the young fruit. The glandular and other hairs that are usually present on the young fruit are shed as it matures. There are no stomata on the epidermis of the fruit (Rosenbaum and Sando, 1920). The mesocarp

the pericarp, take place before fertilization or immediately after it. The growth of the fruit is mainly accomplished by cell enlargement (Ragland, 1934). At first all the cells enlarge almost equally in all directions, but with

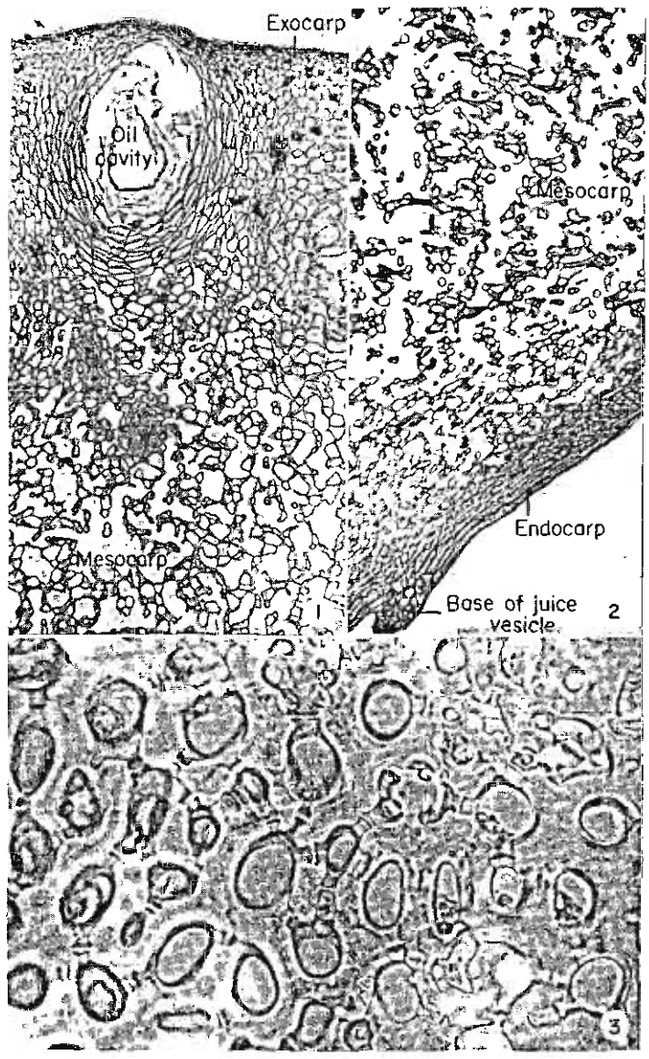


FIG. 212. 1 and 2, Micrographs of portions of the pericarp of *Citrus*. ×40. 1, Outer portion. 2, Inner portion. 3, Micrograph of a section of the endosperm of *Phoenix dactylifera*. ×430.

consists of a thick layer of large thin walled cells which enclose many intercellular spaces. In the early stages of development, soon after pollination, the number of layers in the mesocarp increases rapidly, but the main increase in thickness of the pericarp results from an enormous increase in cell volume in later stages of development. During the process of fruit ripening, some of the cells of the inner and central portion of the carpels may disintegrate. With the development of the ovules, after pollination, the parenchymatous tissue of the placenta grows around the funiculi. This parenchyma continues to grow until it completely encloses the developing seeds (Fig. 211, no. 5). The cells of this tissue are thin-walled and they form a homogeneous tissue; they do not fuse with the pericarp but they adhere to it as well as to the seeds. At first this parenchymatous tissue is firm, but as the fruit ripens the cell walls become thinner and the cells are partly destroyed (Hayward, 1938).

Citrus. In this genus the fruit develops from a syncarpous gynoecium with axile placentation. With the development of the fruit the number of cells throughout the ovary increases and, finally, three strata (Fig. 212, nos. 1, 2) can be distinguished (Schoenichen, 1924; Ford, 1942; Scott and Baker, 1947). The exocarp (flavedo) consists of small, dense collenchyma cells which contain chromoplasts. This tissue contains essential oil cavities (Fig. 212, no. 1). The epidermis consists of very small, thick-walled cells, and in surface view it resembles a cobbled surface; they contain chromoplasts and oil droplets. A few scattered stomata can be found in the epidermis. The mesocarp (albedo) consists of loosely connected, colourless cells; this tissue has a spongy nature and is white because of the numerous air spaces in it. The endocarp is relatively thin and consists of very elongated, thick-walled cells which form a compact tissue. The stalked, spindle-shaped juice vesicles, which fill the locules when the fruit ripens, develop from the cells of the inner epidermis and subepidermal layers (Hartl, 1957). Each juice vesicle is covered externally by a layer of elongated cells which enclose very large, extremely thin-walled juice cells (Fig. 211, nos. 1, 2).

Drupe. In the drupe of *Prunus persica* (Addoms, Nightingale and Blake, 1930) most of the cell divisions, which occur during the development of

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FIG. 211. 1 and 2, *Citrus*. 1, A single juice vesicle. 2, Portion of the vesicle as seen under the microscope. 3 and 4, *Ecballium elaterium*. 3, Diagram of a longitudinally sectioned fruit. 4, A few cells from the inner, white portion of the pericarp. 5, Diagram of a cross-section of the ovary of *Lycopersicon esculentum* after fertilization in which the enlargement of the parenchymatous tissue of the placenta is shown. This tissue forms the fleshy tissue of the fruit. 6, Diagram of a cross-section of the fruit of *Pyrus malus* var. *paradisiaca*. (No. 2, adapted from Schoenichen, 1924; nos. 3 and 4, adapted from Guttenberg, 1926; no. 5, adapted from Hayward, 1938; no. 6, adapted from MacDaniels, 1940.)

bundles are interconnected by branches. It is difficult to distinguish distinctly between the ovary and the hypanthium; generally it is possible to state that the border is between the innermost, prominent bundles of the hypanthium and the dorsal bundles of the carpels.

According to MacDaniels (1940) the ovary wall develops into a parenchymatous exocarp and a cartilaginous endocarp which lines the locules. The endocarp consists of elongated sclereids with very thick walls which almost completely obliterate the cell lumen. These sclereids do not develop close to the dorsal bundles. The endocarp is that part of the fruit that first becomes fully matured, and the last-maturing portion is that which develops from the hypanthium.

In the fruits of *Pyrus communis* and *Cydonia oblonga* groups of brachysclereids (see Chapter 6) develop in the parenchyma.

The banana is also a fruit that develops from an inferior ovary, and it is essentially a berry. From the periphery inwards the following parts can be distinguished: the exocarp, which forms the peel of the fruit, consisting of epidermis, hypodermis and aerenchyma; the mesocarp consisting of large, radially elongated cells which are rich in starch; and the endocarp consisting of the inner epidermis only. The mesocarp, which constitutes the edible part of the fruit, develops from the three to five layers of the carpel wall immediately next to the inner epidermis which lines the locules. These cells first elongate extensively in a radial direction and then they mainly undergo periclinal divisions, although anticlinal divisions also occur.

STRUCTURAL ADAPTATIONS TO SEED DISPERSAL

The seeds of fleshy fruits are usually dispersed by animals that eat the juicy edible portion of the fruit, but there are also fleshy fruits the seeds of which are actively dispersed similarly to those of certain dry, dehiscent fruits. This type of dispersal is called *autochory*. The mechanism of self-dispersal in fleshy fruits is based on turgor pressure. As an example of fruits with this type of mechanism the fruits of *Ecballium elaterium* and *Impatiens* will be described here.

The fruit of *Ecballium* (Fig. 211, nos. 3, 4) is ellipsoidal and is attached to a long stalk, which is bent downward at an acute angle. The pericarp (which develops from an inferior ovary) is fleshy and its outer portion consists of an epidermis and chloroplast-containing parenchyma, in which

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FIG. 213. Fleshy capsule of *Impatiens*. 1, Longitudinally sectioned closed fruit. 2, A fruit, the valves of which have curled inwards and in doing so have ejected the seeds. 3, Portion of a longitudinal section of the pericarp showing the tissue active in opening the fruit. 4, As in no. 3, but as seen in cross-section. (Nos. 1, 3 and 4, adapted from Guttenberg, 1926.)

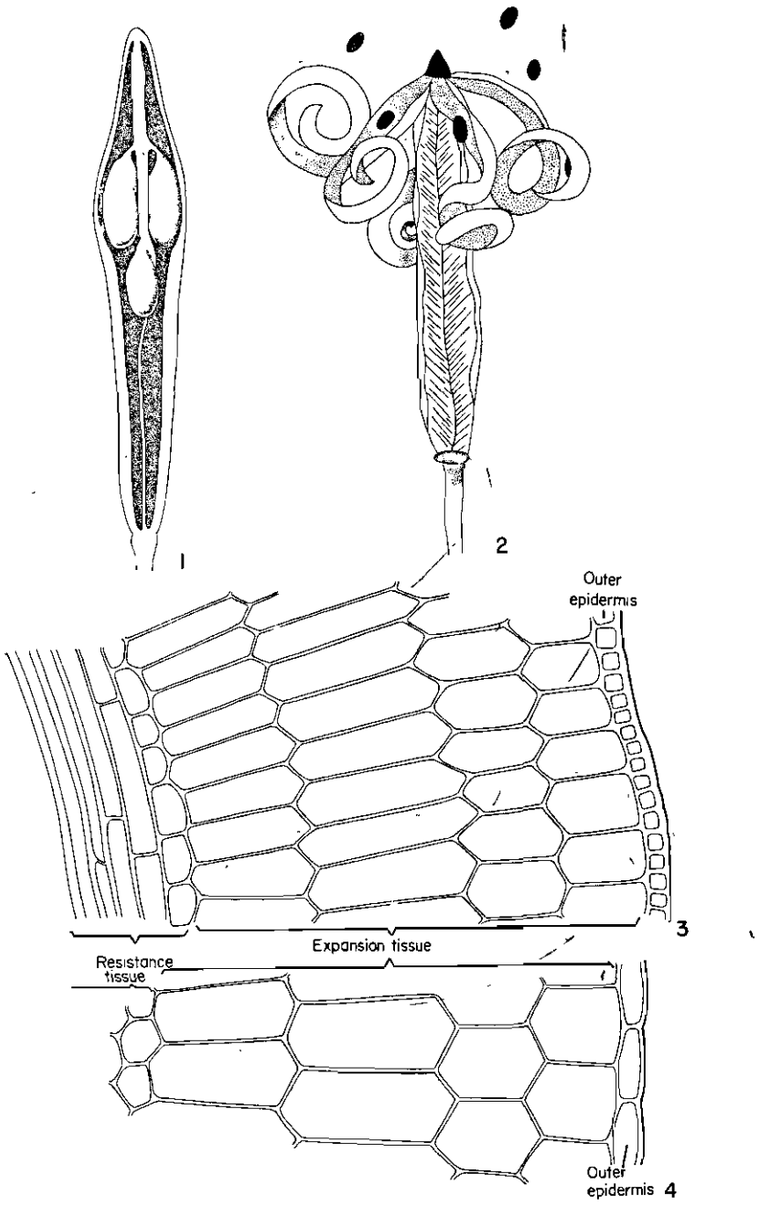
further development of the fruit the enlargement is mainly in a radial direction. This feature is particularly noticeable in the inner portion of the mesocarp. The epidermis (the exocarp) of the mature fruit bears a cuticle and very many unicellular hairs. The mesocarp consists of a non-compact parenchymatous tissue in which the cell dimensions increase from the periphery inwards. In the same direction the shape of the cells also alters, from oval cells in which the longer axis is parallel to the fruit surface to cylindrical, radially arranged cells. The endocarp consists of sclereids and it forms the stone of the fruit. The outer surface of the peach stone is grooved, and in the deep grooves vascular bundles which branch into the mesocarp are found.

FLESHY FALSE FRUITS

The fruit of *Pyrus malus* var. *paradisiaca* may be given as an example of a fleshy fruit developing from an inferior ovary. This fruit has been extensively investigated by numerous workers (MacArthur and Wetmore, 1939, 1941; MacDaniels, 1940; Smith, 1940, 1950) who have reached the conclusion that it mainly develops from the *hypanthium*, i.e. from the basal portion of the perianth and the stamens which are fused and adnated to the carpels. The receptacle participates in the formation of only a very small portion of the basal part of the fruit. The outer parenchyma of the fruit develops from the hypanthium and it contains ten vascular bundles—five belonging to the sepals and five belonging to the petals (Fig. 211, no. 6). These vascular bundles are branched and the branches penetrate into the parenchyma where they form a network. The epidermis is covered by a cuticle which increases in thickness as the fruit develops. In early stages of development of the epidermis stomata may be distinguished, but these later cease to function and are replaced by lenticels (Clements, 1935). In young fruits there are unicellular epidermal hairs, which are shed with the maturation of the fruit. In certain varieties, cork develops on part of the surface of the ripening fruit. The subepidermal tissue, which develops from the outer portion of the hypanthium, consists of a several-layered, thick-walled collenchyma tissue, the cells of which are tangentially elongated. Intercellular spaces develop in this tissue only shortly before fruit maturation, and they are best developed in the more internal ground parenchyma. In still deeper layers the cells are more or less oval and their longer axis is usually radially orientated. This part of the fruit grows most intensely during fruit development, at the start by division of the cells and the enlargement of the derivatives, and later by the increase in cell volume only (Tukey and Young, 1942). The part of the fruit that develops from the ovary is formed by the five folded, but unfused, carpels. Five dorsal carpel bundles are found on the outer side of the locules and ten ventral bundles in the centre (Fig. 211, no. 6). The dorsal and ventral

vascular bundles are embedded. Further inwards the pericarp is white and consists of elliptical cells which are rich in pectic substances and have thick, pitted walls. The longer axis of these cells is at right-angles to the longitudinal axis of the fruit and large intercellular spaces are present between them (Fig. 211, no. 4). Still further inwards is the tissue that envelops the seeds, and which consists of large, vesicle-like, extremely thin-walled cells between which there are no intercellular spaces. These cells have a very thin layer of cytoplasm, and their cell sap contains the glucoside, elaterinidin. This substance is present in such large amounts that in the ripe fruit the osmotic pressure of the sap reaches about 27 atmospheres. As a result of the turgor pressure of the elaterinidin-containing cells, the elastic cells of the white portion of the pericarp expand, and this occurs mainly in the direction at right angles to the longitudinal axis of the fruit. Abscission tissue develops, as the fruit matures, around that part of the stalk that is within the pericarp (Fig. 211, no. 3). At the instant when the pressure which develops in the inner juicy tissue surrounding the seeds exceeds that of the force that keeps the cells of the separation layer together, the stalk is expelled. Simultaneously the pericarp, and especially the white portion of it, contracts and the fruit content—the large juicy cells together with the seeds—is ejected with great force. It was found that the amount of contraction of the pericarp in a transverse direction is 17·3% and in a longitudinal direction 10·8% (Guttenberg, 1926).

The fruit of *Impatiens* is a fleshy capsule in which the septa are extremely delicate. It is cylindrical but somewhat swollen in the upper portion in which the seeds develop (Fig. 213, no. 1). This upper part of the fruit remains inactive, as far as the opening mechanism is concerned, while in the lower portion tension is developed between the outer tissue, which has an expansion potential, and the inner tissue, which offers resistance. When the fruit is mature, the abscission tissue between the carpels ruptures and each valve abruptly curls inwards and, as a result of this, the seeds are expelled (Fig. 213, no. 2). The expansion tissue is located below the outer epidermis which consists of thick-walled cells. This tissue consists of radially elongated parenchyma cells and lacks intercellular spaces (Fig. 213, nos. 3, 4). The cells have a rich sugar content when the fruit ripens and the osmotic pressure in their cell sap reaches 25 to 26 atmospheres. This pressure would result in the rounding of the cells were it not for the resistance offered by the inner portion of the pericarp, which consists of two or three layers of collenchyma cells, the longitudinal axes of which are parallel to that of the fruit (Fig. 213, no. 3). These cells elongate by 10% as a result of the turgor pressure in the outer tissue, and they contract again to the same extent with the opening of the fruit. The outer tissue elongates parallel to the longitudinal axis of the fruit by 32·25% with the opening of the fruit (Guttenberg, 1926).


1
2
Outer epidermis
3
Expansion tissue
Resistance tissue
Outer epidermis
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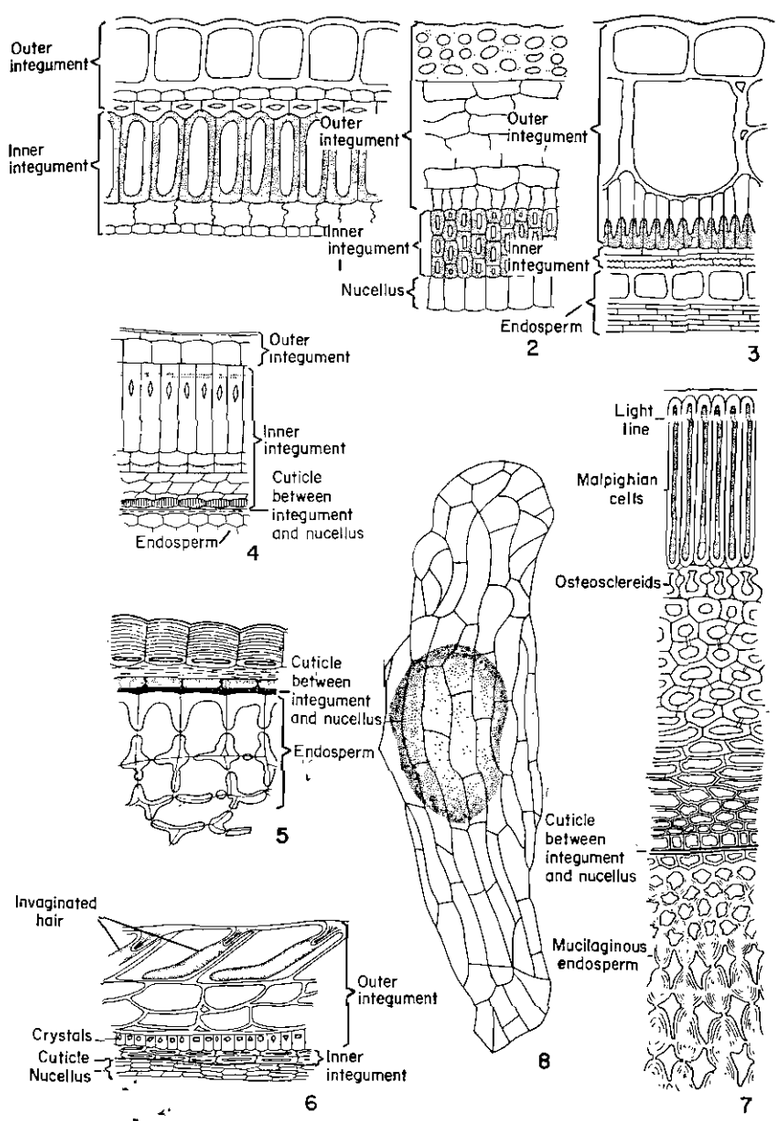

FIG. 214. 1–7, Portions of cross-sections of testae. 1, *Viola tricolor*. 2, *Magnolia macrophylla*. 3, *Sinapis alba*. 4, *Malva silvestris*. 5, *Plantago lanceolata*. 6, *Lythrum salicaria*, showing the invaginated hairs which contain substances that become mucilaginous when moistened, and then the whole structure is pushed out like a finger of a glove. 7, *Ceratonia siliqua*. 8, An entire seed of *Orchis* in which the embryo (stippled) can be seen through the transparent testa. (Nos. 1 and 2, adapted from Eames and MacDaniels, 1947; nos. 3–6, adapted from Netolitzky,

CHAPTER 21

THE SEED

THE seed develops from the ovule. In the mature seed the following parts can be distinguished: the *testa*, which is the seed coat and which develops from one or two integuments; *endosperm*, which may be present in a large or small amount; the *embryo*, which constitutes the partially developed, young sporophyte. In some seeds the endosperm is completely absent and such seeds, as well as those that contain a very small amount of endosperm, are termed *exalbuminous seeds*. In the seeds of certain plants, e.g. *Beta*, the nucellar tissue persists and increases in volume to form the *perisperm*. Several features can be distinguished on the outer surface of the seed. The micropyle may be completely obliterated or it may remain as a distinct pore. In the place where the seed was attached to the funiculus a scar, termed the *hilum*, is present. Water can penetrate with relative ease through the hilum. In anatropous ovules, in which part of the funiculus is fused to the integument, the seed becomes detached together with the fused part of the funiculus which forms a characteristic ridge termed the *raphe*. After the fertilization of the ovule, growths, termed *arils*, develop on the surface of the seeds of certain plants. These growths when they occur on the funiculus, e.g. in *Euonymus* and *Acacia* spp., are often termed *strophioles* and when occurring around the micropyle, e.g. in *Ricinus*, *caruncles*. Arils are very common in tropical and subtropical plants, e.g. in *Intsia bijuga*, *Pithecellobium dulce*, *Durio zibethinus*, *Acacia retivenea*, *Boccia frutescens* and *Myristica fragrans*. Arils are organs that are well adapted to seed dispersal by animals (Corner, 1949). Arils that contain oil, such as those of *Chelidonium majus*, *Luzula villosa*, *Gagea lutea*, *Reseda odorata*, *Galanthus nivalis* and *Ricinus communis*, are elaiosomes (see preceding chapter). In *Chelidonium majus* (Szemes, 1943) the elaiosome (Fig. 217, no. 3) consists of small basal cells and large, sac-like outer cells which store oil, proteins and starch-like grains. Elaiosomes are thought to be connected with seed dispersal by ants.

The testa

Angiosperm ovules have one or two integuments (see Chapter 19). In order to clarify which parts of the integuments take part in the formation of the testa, ontogenetic investigation is necessary. All parts of one or both

integuments may take part in the formation of the seed coat, e.g. *Viola tricolor* (Fig. 214, no. 1), but in most seeds much of the integumental tissue is destroyed and absorbed by the other developing tissues of the seed and then the seed coat develops only from the remaining parts of the integuments. The parts that are destroyed are usually the innermost or intermediate middle layers of the integument. The nucellus may also take part in the construction of the seed coat (Fig. 214, nos. 2, 6). However, in the development of most seeds the nucellus is apparently completely destroyed (Netolitzky, 1926; Eames and MacDaniels, 1947).

In certain seeds, especially those of indehiscent fruits, only the two or three outermost layers of the integument persist. In the mature seed of the Umbelliferae only the outer epidermis of the outer integument remains. In the seeds of certain genera of the Compositae, e.g. *Lactuca* (Fig. 206, nos. 3, 4), the integuments are represented only by a thin layer of obliterated cells which persists beneath the cypsela coat. The innermost layers of the latter coat also disintegrate (see Chapter 20). In the seeds of certain monocotyledons, e.g. *Zea*, the integuments are completely destroyed. In seeds developing from ovules with two integuments, the two integuments may be present in the testa or only two or three of the outermost layers of the outer integument may remain. In such seeds the inner integument may constitute the major portion of the seed coat (Fig. 214, no. 4), or the outer one may be the better developed and be especially adapted for protection while the inner is non-specialized (Fig. 214, no. 3). The former type is characteristic of the Malvaceae, Violaceae, Hypericaceae and Tiliaceae, and the latter of the Cruciferae, Papaveraceae, Berberidaceae and certain genera of the Liliaceae, Iridaceae and Araceae. In the Onagraceae, Lythraceae, Aristolochiaceae and others, protective layers develop from both integuments, and the entire nucellus or its outermost layers only also take part in the formation of the seed coat (Fig. 214, no. 6). In most of the Leguminosae, Ranunculaceae and certain genera of the Liliaceae and Amaryllidaceae the inner integument and the nucellus are completely obliterated. In the seeds of only a few plants in which the ovule is surrounded by a single integument does the entire integument form the seed coat. Usually only a few of the outermost cell layers and the inner epidermis persist, e.g. in the Plantaginaceae (Fig. 214, no. 5) and Polemoniaceae.

HISTOLOGICAL STRUCTURE OF THE TESTA

There are vast differences in histological structure of the seed coats of the different plants. The simplest type of seed coat structure occurs in the seeds of the Orchidaceae where the seed coat consists of a single layer of elongated cells which originate from the outer integument. An air space is present (Fig. 214, no. 8) between this membranous coat and the un-

differentiated embryo. This feature enables the dispersal of the seeds, which are about a quarter of a millimetre long, by wind.

The structure of seed coats that are very hard or fleshy, and especially of those that are sculptured, is complicated.

In the seeds of some plants, e.g. certain genera of the Leguminosae, the testa is covered by a very thick cuticle which prevents the passage of water and air as long as it is undamaged.

In the seed coats of certain plants, a layer of radially elongated cells, which are palisade-like but devoid of intercellular spaces, may be present. These cells have been termed *Malpighian cells* after the investigator who first described them. Because of their shape and the thickness of their walls, these cells are also termed *macrosclereids*. The thickness of the walls is characteristically not equal throughout, and the walls may consist of cellulose only or of lignin or cutin as well. Malpighian cells are especially characteristic of the Leguminosae where they constitute the outer epidermis. In seeds of the Leguminosae, the cell lumen of the Malpighian cells is usually widest at the base of the cell. In *Cercidium floridum*, the walls of these epidermal cells have been observed to be traversed by plasmodesmata (Scott *et al.*, 1962). In a cross-section of the seed coat, a thin line which runs across the cells and parallel to the surface of the seed close to the cuticle can be distinguished. This is due to the fact that, along this line, the light refraction differs from that in other parts of the cells. This line is termed the *light line* or *linea lucida* (Fig. 214, no. 7). In the seeds of certain species the light line is a result of deposition of wax globules in the cells (Eames and MacDaniels, 1947). Non-epidermal Malpighian cells are mainly found in families other than the Leguminosae, e.g. in the seeds of *Gossypium* (Fig. 216, no. 4) and *Malva* (Fig. 214, no. 4).

In the seeds of many of the Leguminosae one or more layers of cells with unusual shape are found below the Malpighian cells; these cells may be funnel- or bone-shaped, for instance, and because they are also thick-walled, they are termed *osteosclereids*. They may, like the epidermal cells, contain pigments or be devoid of them. In certain species of *Phaseolus* these cells also contain crystals of oxalate salts (Netolitzky, 1926). The greater portion of the inner tissue of the integuments disintegrates and the outer cells develop at the expense of the contents of this tissue. The cells that remain after this process of disintegration may sometimes be thick-walled. In the testa of many seeds the inner epidermis may be present and sometimes a cuticle can be distinguished between the testa and the remains of the nucellus or endosperm (Fig. 214, nos. 4–7). Relatively well-developed vascular bundles may be found in the testa of certain plants (*Arachis*), while in others (*Pisum* and *Lathyrus*) they can hardly be distinguished. In leguminous seeds the nucellus apparently disappears completely.

Corner (1951) has drawn attention to the value of the structure of the seed coat in the taxonomy of the Leguminosae. The cells of the testae

of the seeds of other families also have different characteristic shapes, wall thickenings, etc. The testa of *Phoenix* consists of thin-walled cells only. During the course of seed development, the number of cell layers of the integuments, and especially of the inner integument, decreases.

The structure and development of the seed of *Lycopersicon esculentum* has been described by Souèges (1907) and is of great interest. In the thick integument of the young *Lycopersicon* seed the following four parts can be distinguished: an outer epidermis; an intermediate parenchymatous tissue in which inner and outer zones can be distinguished; an inner epidermis which contains pigment (Fig. 215, no. 1). With the development and enlargement of the seed, the cells of the outer parenchymatous zone increase in number, and thickenings develop in the inner tangential walls and at the base of the radial walls of the outer epidermal cells (Fig. 215, nos. 2, 3). When the seeds are partially mature the outer epidermal cells are seen

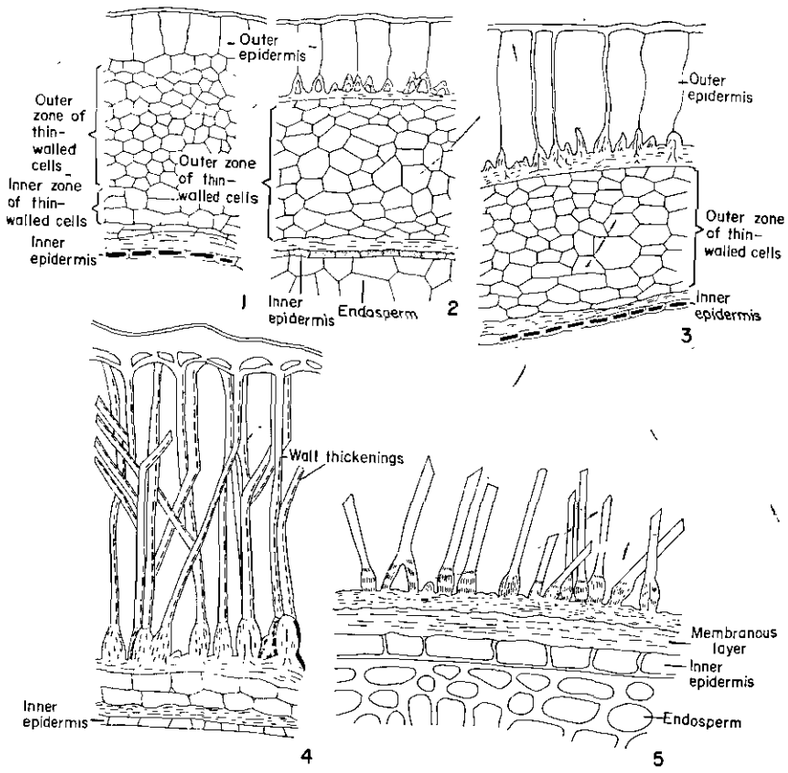

FIG. 215. Portions of cross-sections of the testa of *Lycopersicon esculentum* showing different stages of development. (Adapted from Hayward, 1938.)

to be very elongated in a radial direction, and longitudinal wall thickenings, which appear more or less in the angles of the cells, are developed. These thickenings increase in length till they reach the outer tangential wall (Fig. 215, no. 4). With the final ripening of the seeds the thin parts of the radial and outer walls rupture, and only the thickened strands remain. These strands form the hair- or scale-like structures that cover the surface of the mature seed (Fig. 215, no. 5). Together with this process the intermediate parenchyma disintegrates gradually in a centrifugal direction from the inner zone. In the mature seed nothing remains of this parenchyma except for the crushed walls which form a more or less uniform membranous layer. The pigment-containing inner epidermis remains and it forms the inner border of the testa.

In certain seeds, e.g. those of *Linum usitatissimum*, in outer layer, which becomes mucilaginous when in contact with water, s developed. In the mature seed of *Linum* several zones may easily be distinguished (Hayward, 1938). The outer epidermis is covered by a cuticle. With the development of the seed coat a mucilaginous substance develops on the inner side of the thick outer wall of the epidermal cells so as almost completely to fill the cell lumen (Fig. 216, nos. 1, 2). This substance, which exhibits a stratified texture, swells very greatly when it absorbs water. The middle lamellae between the cells are not sufficiently elastic to accommodate this swelling and so they rupture and the outer cutinized wall layers, which are covered with cuticle, become raised and crack. Below the epidermis there are one or two layers of cells whose lumina appear circular in a surface view of the seed. Below these cells is a layer of elongated, pitted sclerenchyma cells (Fig. 216, no. 2). The orientation of these cells is parallel to the longitudinal axis of the seed. Still further inwards there are two zones of parenchyma cells which are elongated at right-angles to the sclerenchyma cells. These parenchyma cells contain much starch, which is absorbed by the other tissues during the development of the seed, and the cells themselves become crushed and obliterated. The cells of the innermost layer of the testa are cubical or polyhedral with thick pitted walls and they contain in their cell lumina, the pigment that determines the colour of the seed.

The surface of the seeds of different species may have special and characteristic features, which are used in classification. Hairs, ribs, folds, spines or hooks usually develop from the epidermis of the testa alone, but there are instances in which subepidermal cells take part in their formation. The fibres of *Gossypium*, for example, are epidermal cells which elongate to form hairs (Fig. 216, no. 4). Sometimes the testa is expanded to form a wing-like structure of thin-walled cells, which become filled with air. Such winged seeds (*Fibigia clypeata*, for example) are easily distributed by wind. Many seeds, e.g. of most genera of the Asclepiadaceae, Apocynaceae and Tamaricaceae, bear tufts of hairs which facilitate dispersal by wind. In some such seeds, e.g. those of *Tamarix* (Fig. 217, no. 1) and *Myricaria*,

is termed *hypogeal germination.* In this type of germination the terminal bud of the embryo is pushed out through the soil by the elongation of the *epicotyl* which is the stem above the cotyledons (Fig. 219, nos. 1, 2).

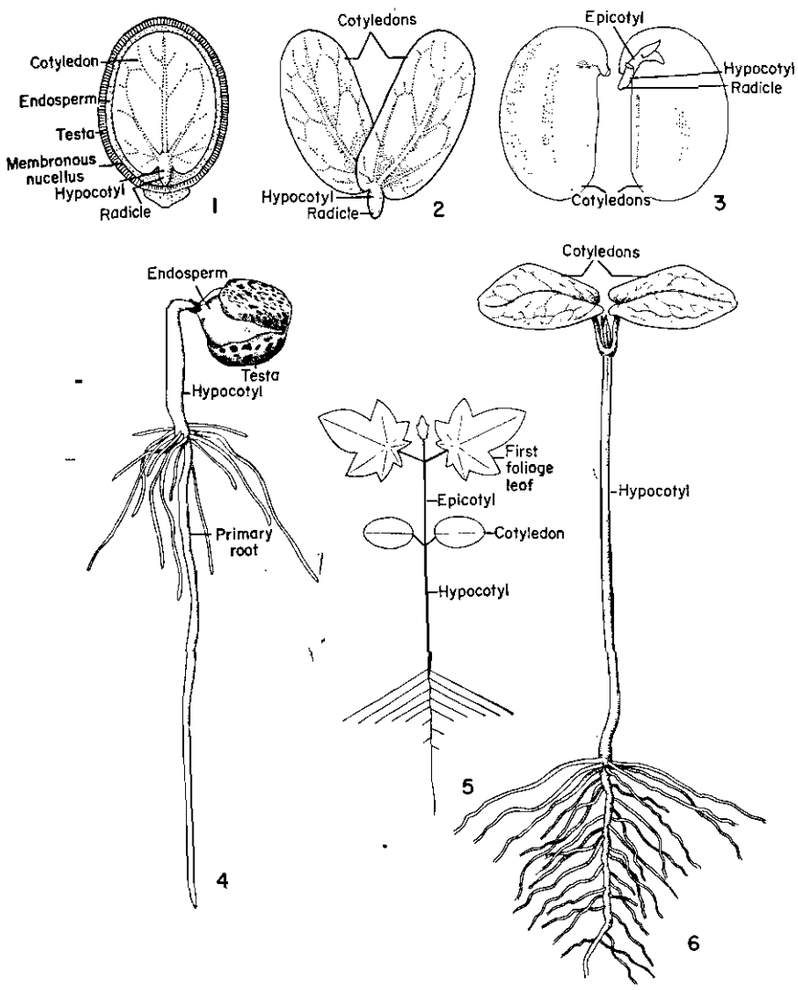

FIG. 218. 1, Longitudinally sectioned seed of *Ricinus communis*. The protuberance at the base of the seed is the caruncle. 2, Embryo of *Ricinus communis* with cotyledons opened out. 3, Embryo of *Phaseolus vulgaris* with cotyledons spread out. 4–6, Seedlings of *Ricinus communis* at different stages of development. 4, Emergence of the primary root and hypocotyl. 5, Schematic diagram of a seedling that has already produced foliage leaves. 6, Young seedling with cotyledons expanded. (Adapted from Troll, 1948.)

the hairs undergo hygroscopic movements—they spread when dry and converge when wet. This movement is brought about by the specialized structure (Fig. 217, no. 2) of the basal portion of the abaxial wall of each hair (Guttenberg, 1926).

The testa of certain plants is juicy. In *Punica*, for example, the juicy edible layer develops entirely from outer epidermal cells which elongate

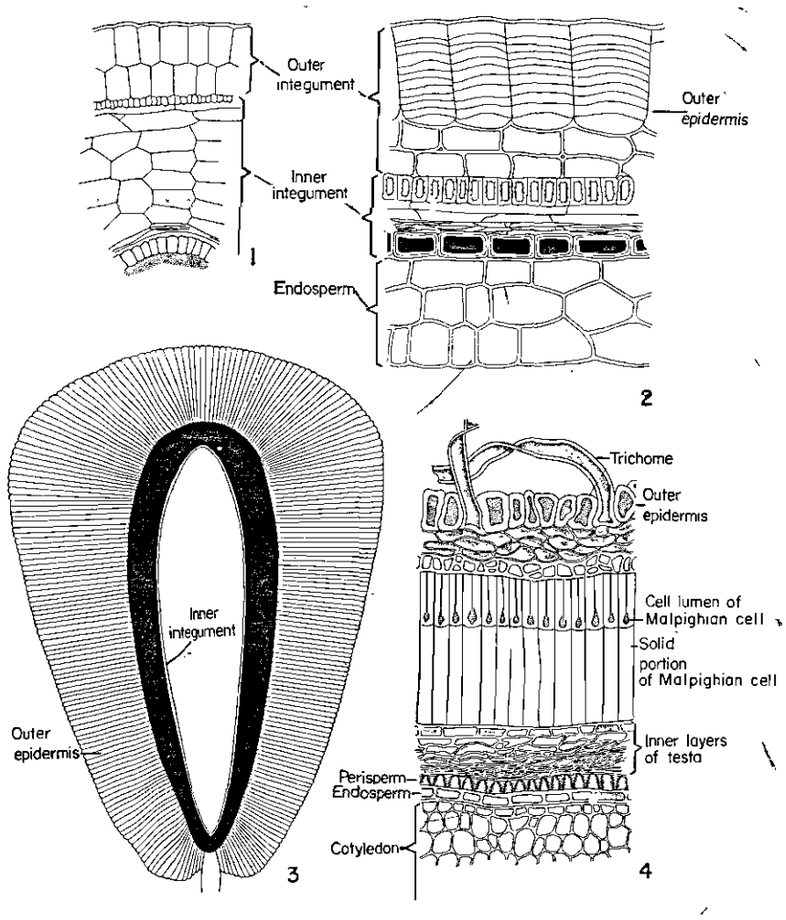

FIG. 216. 1 and 2, Portions of cross-sections of the testa of *Linum usitatissimum*. 1, Developing testa. 2, Mature testa. 3, Diagram of a longitudinal section of the seed of *Punica granatum* showing the radially elongated cells of the outer epidermis of the testa; these cells form the fleshy part of the seed. The inner portion of the outer integument is sclerenchymatous (solid black.) 4, Portion of a cross-section of the testa of *Gossypium*. (Nos. 1 and 2, adapted from Hayward, 1938; nos. 3 and 4, adapted from Eames and MacDaniels, 1947.)

to a very large extent in a radial direction. The sap of these cells develops a turgor pressure which preserves the characteristic external shape of these seeds (Fig. 216, no. 3).

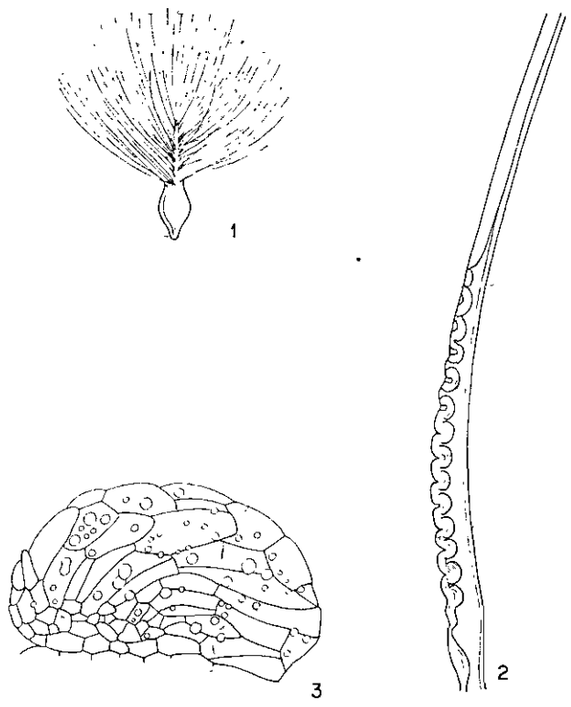

FIG. 217. 1 and 2, *Tamarix*. 1, An entire seed, with tuft of hairs. 2, The base of a single hair of the tuft, enlarged to show the characteristic structure of the abaxial wall. 3, Elaiosome of *Chelidonium majus*. (No. 3, adapted from Szemes, 1943.)

The endosperm

The development and types of endosperm have been discussed in Chapter 19; here the mature endosperm will be briefly described. The endosperm tissue in the developing seed may consist of thin-walled cells with large vacuoles, which do not contain reserve substances. Such an endosperm is entirely or partially absorbed by the developing embryo, e.g. *Lactuca*. In many other seeds, e.g. those of *Ricinus* and the Gramineae, the endosperm functions as a storage tissue. An endosperm of this type may consist of thin-walled cells and then the reserve material is located within the cell, or it may consist of thick-walled cells and then the walls themselves con-

In addition to the functions of storage and photosynthesis, cotyledons may bring about the breakdown, absorption and transport of nutrient substances from the endosperm to the developing embryo. Cotyledons fulfilling such functions occur in the monocotyledons such as *Allium cepa*, *Phoenix* and in the Gramineae. During the germination of the seed of *Allium cepa* (Fig. 219, nos 3–5), the cotyledon elongates and pushes the radicle tip out of the seed. The emerging root tip is usually directed upward at first, owing to the shape of the seed, and it becomes positively geotropic only at a later stage. The sharp bend thus caused by the change in the direction of growth is known as the "knee" (Fig. 219, no. 5). The other end of the cotyledon remains within the seed where it is in contact with the endosperm and where it functions as an *haustorium* for the absorption of nutrients. The exposed part of the cotyledon becomes green and may carry out photosynthesis. In the final stage of the germination process the remains of the testa and endosperm are shed from the absorbing end of the cotyledon and the cotyledon then straightens.

The germination of the seed of *Phoenix* (Fig. 219, nos. 6–11) is, in general, similar to the above. Here, that end of the cotyledon that remains within the endosperm develops into an haustorium which gradually enlarges with the increased disintegration of the endosperm (Fig. 219, no. 10). In *Phoenix* the terminal bud of the embryo shoot is concealed in the sheathing part of the cotyledon.

In the Gramineae the cotyledon is shield-like and has therefore been termed the *scutellum*. This organ remains within the caryopsis in contact with the endosperm from which it absorbs the nutrient substances (Fig. 220, nos. 1, 2). The epidermal cells of the scutellum that border on the endosperm are elongated at right-angles to the surface of the scutellum. Scattered glands are present between these epidermal cells (Sargant and Robertson, 1905). Here, also, the first organ to emerge from the caryopsis is the radicle. The shoot apex is enclosed in a sheath-like leaf termed the *coleoptile*. At first, the coleoptile grows at the same rate as the bud within it. Only after it reaches a certain length do the internodes of the plumule elongate and the foliage leaves enlarge so that they emerge to the exterior through a rupture which forms at the upper end of the coleoptile.

The nature of the coleoptile has been variously interpreted (Eames, 1961). Some authors regard it as the first true leaf, while others believe it to be part of the cotyledon. Various opinions also exist as to the nature of the axial part of the embryo below the coleoptile (Eames, 1961). It is considered by some authors to be a complex structure formed by the fusion of parts of the cotyledon with the hypocotyl, and thus this part of the axis is termed, by them, the *mesocotyl*. Those investigators who consider the coleoptile to be the first leaf regard the above part of the embryonal axis as the first internode. The sheath that surrounds the endogenously developed root is termed the *coleorrhiza*. This sheath is interpreted as being

stitute the reserve substance. In the former type mainly starch grains and proteins are the stored substances. There are two main forms in which proteins may be stored in the endosperm—in an amorphous form (glutens), or in the form of aleurone grains. Aleurone grains consist of a protein crystalloid and a spherical body (the globoid) which contains salts of calcium, magnesium and phosphorus in an organic compound. In the caryopses of cereals glutens are found in the starch cells and aleurone grains are restricted to the outermost layer of endosperm cells (the aleurone layer). In *Ricinus*, however, aleurone grains occur throughout the entire endosperm. In endosperm in which there is no starch, oils and fats may be present as reserve substances. (See also Chapter 2.)

Cell walls that constitute reserve material, e.g. in the seeds of *Phoenix* (Fig. 212, no. 3) and *Diospyros*, usually consist of hemicelluloses and other similar carbohydrates. In *Phoenix*, Meier (1958) recorded that these walls apparently contain, in addition, about 6% of cellulose. These cells have a very thick secondary wall.

Some seeds, e.g. those of *Ceratonia*, have a *mucilaginous endosperm* (Fig. 214, no. 7). A stratified thickening of the walls of these endospermal cells can be distinguished. These walls become more or less mucilaginous when in contact with water. In the dry seeds these endospermal cells are hard and, during germination, they function both as a swelling and nutritional tissue (*Netolitzky, 1926*).

Seedlings

With the germination of the seed, the testa ruptures at the micropylar end and the radicle emerges. Generally, the radicle penetrates into the soil, develops root hairs and often lateral roots. After this, further rupturing of the testa takes place.

In many seeds the cotyledons and shoot apex emerge while the hypocotyl elongates as a result of intercalary growth. This type of germination is termed *epigeal germination;* examples of such germination can be seen in *Helianthus*, *Raphanus*, *Phaseolus* and *Ricinus* (Fig. 218, nos. 4–6).

The cotyledons of plants in which the germination is epigeal may vary in form and function. The cotyledons of *Phaseolus vulgaris*, for example, are very thick and function as storage organs (Fig. 218, no. 3). These cotyledons wither early and are shed. The cotyledons of many other dicotyledonous plants in which the germination is epigeal are thinner structures, which, when appearing above ground, more closely resemble foliage leaves (Fig. 218, no. 6).

In many other plants, e.g. *Vicia*, *Pisum sativum* and *Quercus*, the thick cotyledons, which contain reserve materials, remain within the testa and the hypocotyl elongates only slightly or not at all. This type of germination

embryonic organs, such as the coleorrhiza, for example (Roth, 1955; Brown, 1960; Eames, 1961; Foard and Haber, 1962; Negbi and Koller, 1962). A provascular system can be distinguished within the embryo, and it has been described in detail by Avery (1930).

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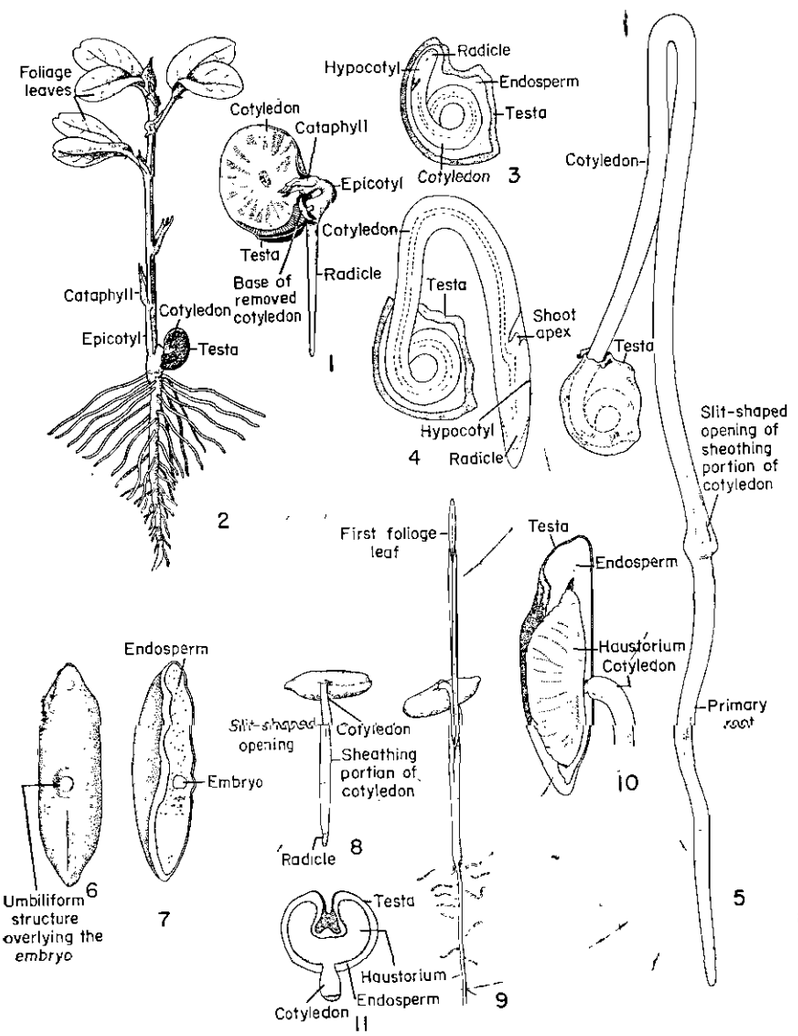

FIG. 219. 1 and 2, Seedlings of *Vicia faba*. 1, Longitudinally sectioned germinating seed. 2, A young plant. 3–5, Seed and seedling of *Allium cepa*. 3, Longitudinally sectioned seed. 4, Germinating seed sectioned longitudinally. 5, Developing seedling. 6–11, Seed and seedling of *Phoenix dactylifera*. 6, An entire seed. 7, Longitudinally sectioned seed. 8, Germinating seed. 9, Mature seedling which has already produced foliage leaves. 10, Longitudinally sectioned seed which has germinated and has already produced a mature seedling. 11, Cross-section of seedling at the same stage as in No. 10. (Adapted from Troll, 1948.)

apical cell, the single initial present in the apical meristem of some roots and shoots; typical of many lower vascular plants.
apocarpy, that condition in a flower and ovary where the carpels are free.
apomixis, process of reproduction in the ovule without fertilization.
apposition (of cell wall), wall growth as a result of successive addition, layer on layer, of wall material.
aril, a fleshy growth on the seed developing from the base of the ovule. Sometimes also used to refer to outgrowths developing from other parts of the ovule.
asterosclereid, a branched sclereid.
atactostele, a stele which consists of vascular bundles scattered throughout the ground tissue as in the Monocotyledoneae.
autochory, seed dispersal by means of a self-dispersal mechanism.
axial organ, the root, stem, inflorescence or flower axis without their appendages.

back wall, that part of the guard-cell wall which is adjacent to the subsidiary or ordinary neighbouring epidermal cells.
bark, a collective term for all the tissues outside the vascular cambium.
bark, outer, *see* **rhytidome.**
basipetal, proceeding towards the base.
bifacial leaf or **dorsiventral leaf,** a leaf in which palisade parenchyma is present on one side of the blade and spongy parenchyma on the other.
body, primary, that part of the plant which develops from the primary meristems, apical and intercalary.
body, secondary, that part of the plant, comprising the secondary vascular tissues and periderm, which is added to the primary body as a result of the activity of the lateral meristems, i.e. the cambium and phellogen.
brachysclereid or **stone cell,** a short, more or less isodiametric sclereid.
bulliform, cell, an enlarged epidermal cell common in the leaf of the Gramineae; rows of such cells occur along the leaf.
bundle sheath, a layer or layers of cells surrounding the vascular bundles of leaves; may consist of parenchyma or sclerenchyma.
bundle sheath extension, a strip of ground tissue present along the leaf veins and extending from the bundle sheath to the epidermis; may be present on both sides of the vein or on one side only and may consist of parenchyma or sclerenchyma.

callose, a polysaccharide present in sieve areas, walls of pollen tubes, walls of fungal cells, etc.
callus, (1) a layer of callose which forms on sieve areas; (2) the tissue formed as a result of wounding or a tissue developing in tissue culture.
calyptrogen, a term arising out of the histogen theory. In the root apex that meristem from which the root cap develops independently of all other initials of the apical meristem.
cambium, non-storied, a cambium in which the fusiform initials, as seen in tangential section, partially overlap one another and are not arranged in horizontal rows.
cambium, storied, a cambium in which the fusiform initials, as seen in tangential section, are arranged in horizontal rows.
cambium, vascular, a lateral meristem from which the secondary vascular tissues, i.e. secondary xylem and phloem, develop.
cambium-like transitional zone, a cyto-histological zone visible in some shoot apices (see pp. 55–59).
carpophore, the split axis of a cremocarp to which the mericarps remain attached after they become separated from each other.

either part of the scutellum or part of the axis. Another characteristic feature of the grass embryo of certain genera is the presence of the *epiblast*. This is a small scale-like organ opposite the scutellum, and it is devoid of

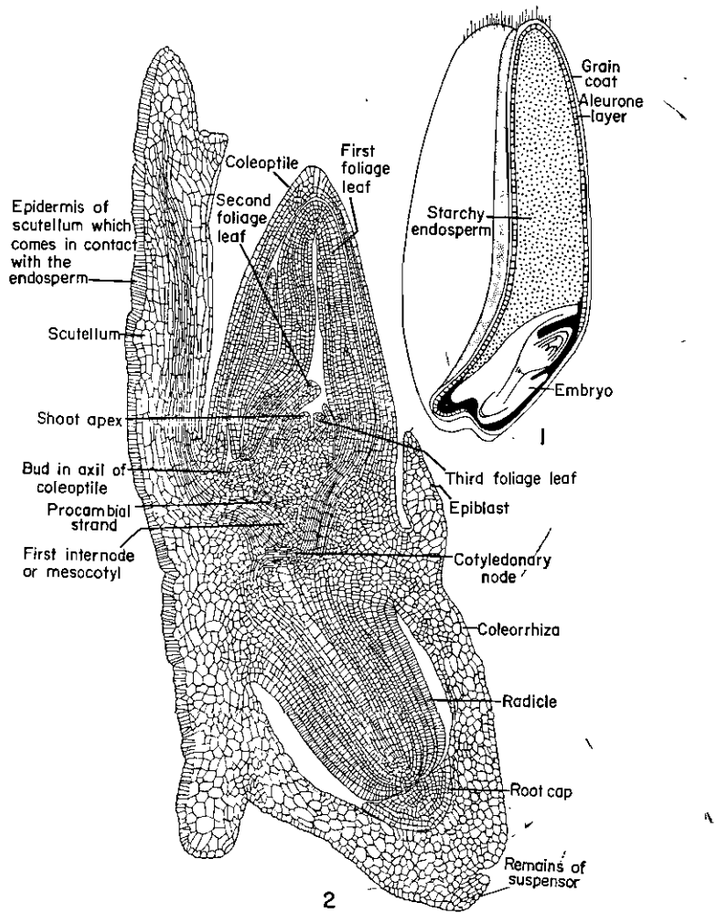

FIG. 220. 1, Grain of *Triticum* sectioned longitudinally in the region of the groove. 2, Longitudinal section of the embryo of *Triticum*. (No. 1, adapted from Esau, 1953; no. 2, adapted from Hayward, 1938.)

vascular supply. Different opinions exist as to the homology of the epiblast. According to some investigators it represents a vestigial second cotyledon, while others regard it as being an outgrowth or part of other

cuticle, a layer of cutin, a fatty substance which is almost impermeable to water, on the outer walls of the epidermal cells.
cuticle layer, the outer portions of the epidermal walls which are impregnated with cutin.
cutinization, the deposition of cutin in cell walls.
cylinder, central or **vascular,** that part of the axis of the plant consisting of vascular tissue and the associated parenchyma. Equivalent to the term *stele*, but without the evolutionary connotation associated with this term.
cystolith, a specific outgrowth of the cell wall on which calcium carbonate is deposited. Characteristic of certain families, e.g. the Moraceae.
cytochimera, a combination, in a single plant organ, of tissues the cells of which are of different chromosome number.
cytokinesis, the process of cell division which results in the formation of two separate cells.

dermatogen, *see* **histogen.**
diacytic type, a specific pattern of arrangement of the guard cells and other epidermal cells adjacent to them (see p. 151).
diaphragm, a cross partition in an elongated air cavity.
diarch, that condition in the primary xylem of the root where there are two protoxylem strands.
dictyostele, a siphonostele in which the leaf-gaps are large and partly overlap one another so as to divide the stele into separate bundles in each of which the phloem surrounds the xylem.
differentiation, the physiological and morphological changes leading to specialization which occur in a cell, tissue, organ or entire plant during the process of development from a meristematic or juvenile state to a mature one.
diffuse-porous wood, *see* **wood.**
dorsiventral leaf, *see* **bifacial leaf.**
druse, a compound crystal, more or less spherical in shape and in which the many component crystals protrude from the surface.
duct, an elongated space formed schizogenously, lysigenously or schizo-lysigenously and which may contain secretory substances or air.
duramen, *see* **heartwood.**

ectodesma, a plasmodesma appearing in the outer walls of the epidermis.
ectoplast, *see* **plasmalemma.**
elaioplast, an oil-producing and storing leucoplast.
elaiosome, an outgrowth on a fruit or seed that contains large oil-storing cells.
emergence, a projection of the surface of a plant organ which consists not only of epidermal cells or parts of them, but also of cells derived from underlying tissues.
endarch xylem, in reference to the direction of maturation of the elements in a strand of primary xylem; a strand in which the first-formed elements (the protoxylem) are closest to the centre of the axis, i.e. the maturation is centrifugal.
endocarp, the innermost layer of the pericarp (fruit wall).
endogenous, developing from internal tissues.
endosperm, a nutrient tissue formed within the embryo sac of the Spermatophyta.
endothecium, in the pollen-sac wall; a layer of cells with characteristic wall thickenings situated below the epidermis.
epiblast, a small growth present opposite the scutellum in the embryo of some Gramineae.
epiblem, the outermost cell layer (epidermis) of roots, as termed by some workers.
epicotyl, the stem of an embryo and seedling above the cotyledons.

GLOSSARY OF TERMS

This glossary includes most of the terms used in this book. Many terms which occur only once are defined only where they are mentioned.

abaxial, directed outwards from the axis.

abscission zone, that zone containing the tissues which bring about the abscission of organs such as leaves, fruits and flowers.

accessory or subsidiary cell, an epidermal cell which borders on a guard cell of the stoma and which differs from the ordinary epidermal cells.

acropetal, proceeding towards the apex.

actinostele, a protostele in which the xylem, as seen in cross-section, is star-shaped.

adaxial, directed towards the axis.

adnation, concrescence of organs or tissues of different nature.

adventitious organ, an organ which developed in an unusual position.

aerenchyma, a parenchymatous tissue characterized by the presence of large intercellular spaces.

aggregate fruit, a fruit developing from an apocarpous ovary in which the development of the carpels is independent, each having its own pericarp, but with the ripening of the fruit, a single unit is formed.

albuminous cell, certain cells in the phloem rays or in the phloem parenchyma of Gymnospermae which are connected morphologically and physiologically to the sieve elements. Unlike the companion cells of the Angiospermae, these cells do not usually arise from the same cell as the sieve element.

alburnum, *see* **sapwood.**

aleurone grain, a characteristic structure of reserve protein present in the seeds of numerous plants. In the endosperm of certain plants such grains are found in the outermost cell layer which is then termed the *aleurone layer.*

amphicribral vascular bundle, *see* **vascular bundle.**

amphiphloic siphonostele, *see* **siphonostele.**

amphivasal vascular bundle, *see* **vascular bundle.**

amyloplastid, a leucoplastid which has become specialized to store starch.

androecium, the collective term for all the stamens of a flower.

androgynophore, a stalk-like elongation of the floral axis between the perianth and stamens, which elevates the androecium and gynoecium.

anisocytic type (of stomata), a specific pattern of arrangement of the guard cells and other epidermal cells adjacent to them (see p. 150).

anisotropic, having different properties along different axes. Optically—having different optical properties, showing birefringence.

anomocytic type (of stomata), a specific pattern of arrangement of the guard cells and other epidermal cells adjacent to them (see p. 149).

anthesis, the time of maturation of the male and female organs of the flower.

anticlinal, perpendicular to the surface.

antipodal cells, the cells of the female gametophyte present at the chalazal end of the mature embryo sac of the Angiospermae.

aperture (of pollen grain), an area of characteristic shape in which the exine is completely lacking or in which nexine alone is present; the pollen tube emerges via such an area.

apex, the terminal portion of the shoot or root in which the apical meristem is located.

growth, intrusive, that type of growth in which the growing cell penetrates between existing cells and in which new areas of contact are formed between the penetrating and neighbouring cells.
growth, mosaic, a theory concerning primary wall growth (see p. 30).
growth, multinet, a theory concerning primary wall growth (see p. 30).
growth, symplastic, the process of uniform growth of neighbouring cells so that the adjacent walls do not alter position relative to each other and no new areas of contact are formed.
growth ring, a clearly distinguishable region in the secondary xylem or phloem which is formed during a single growth season.
guard cells, a pair of specialized epidermal cells which, together with the aperture between them, form the stoma.
gum, a general term for the substances formed on the disintegration of cells, mainly carbohydrates.
gummosis, a pathological condition which is expressed by the formation of gum.
guttation, the secretion of water, in a liquid form, from plants.
gynoecium, all the carpels of a single flower.
gynophore, an elongation of the floral axis between the stamens and the carpels, thus forming a stalk which elevates the gynoecium.

haplostele, a protostele in which the xylem, as seen in cross-section, is more or less circular.
hardwood, a common name for wood of the Dicotyledoneae.
haustorium, a specialized organ that draws nutriment from another organ or tissue.
heartwood or **duramen,** the inner layers of wood in the growing tree or shrub, which have lost the ability to conduct and no longer contain living cells. Generally darker in colour than sapwood.
hilum, (1) that portion of a starch grain around which the starch is laid down in layers; (2) the scar present on a seed resulting from its abscission from the funiculus.
histogen, a term used to refer to those initials in the apical meristem of the root and shoot which are predestinated to give rise to a particular and constant tissue system of the organ concerned. Hanstein distinguished three histogens: *dermatogen* which gives rise to the epidermis; *periblem* which gives rise to the cortex; *plerome*, which gives rise to the vascular cylinder.
hydathode, a structure sometimes of glandular nature, through which water is secreted in liquid form; found mainly on leaves.
hygrochastic process, manner of fruit opening or of the movement of other organs, as a result of water uptake; usually connected with the dispersal of seeds or spores.
hypoblast, a term used for the suspensor of the mature grass embryo.
hypodermis, a specific layer or layers of cells beneath the epidermis, which differ structurally from the tissue below them. In the narrow sense of the term, refers only to such layers which arise from a meristem other than the protoderm.
hypophysis, one of the cells of the embryo in its early stages of development (see p. 432).
hypsophyll, an inflorescence bract; a vestigial leaf or any other leaf having a structure different from that of a foliage leaf and occurring near the top of the shoot.

idioblast, a specific cell which is clearly distinguished from the other cells of the tissue in which it appears, either by size, structure or content.
initial, (1) in meristems; a cell which remains within a meristem and which adds cells to the plant body as a result of cell division; (2) of an element; a meristematic cell which differentiates into a mature specialized element.
integument, an envelope surrounding the nucellus of the ovule.

caruncle, an outgrowth of the integuments at the micropylar region.
caryopsis, a fruit in which the pericarp and testa are fused; characteristic of the Gramineae.
Casparian strip, a band-like structure in the primary wall containing lignin and suberin. Especially characteristic of the endodermal cells of roots where the band is present in the anticlinal walls, both radial and transverse.
cataphyll, a leaf which appears on the basal portions of shoots, e.g. scales on rhizomes, bud scales, etc.
cell plate, that part of the wall which develops between the two daughter nuclei during telophase.
central mother cells a cyto-histological zone of the shoot apex (see pp. 53–57).
chalaza, that region in the ovule where the nucellus and integuments connect with the funiculus.
chimera, a combination in a single plant organ of tissues of different genetic composition.
chlorenchyma, a chloroplast-containing parenchyma tissue such as the mesophyll and other green tissues.
chlorophylls, the green pigments present in the chloroplastids.
chloroplastid, a specific protoplasmic body in which photosynthesis takes place; contains among other pigments, the chlorophylls.
chromoplastid, a specific protoplasmic body containing pigments other than chlorophyll; usually containing carotenoids.
cluster, referring to the arrangement of vessels as seen in cross-section of the secondary xylem; several vessels grouped together in both radial and tangential direction.
coenocyte, a group of protoplasmic units; a multinucleate structure. In Spermatophyta often used to refer to multinucleate cells.
cohesion, concrescence of organs or tissues of the same nature.
coleoptile, the sheath surrounding the apical meristem and leaf primordia of the grass embryo.
coleorrhiza, the sheath which surrounds the radicle of the grass embryo.
collenchyma, the supporting tissue of young organs; consisting of more or less elongated cells the walls of which are usually unequally thickened.
colleter, a multicellular hair comprising stalk and head, and having a sticky secretion.
columella, the central portion of the root-cap in which the cells occur in longitudinal files.
companion cell, a specialized parenchyma cell associated with the sieve tube member in the phloem of Angiospermae; it originates from the same mother cell as the sieve tube member and has a physiological connection with it.
complementary cells, a loose tissue formed towards the periphery by the phellogen of the lenticel; the cells may or may not have suberized walls.
connective, the tissue present between the two lobes of an anther.
cork, see *phellem* in **periderm.**
cork cell, (1) a dead cell which arises from the phellogen and whose walls are impregnated with suberin; has a protective function as the walls are impermeable to water and gases; (2) in an epidermis—a short cell with suberized walls; characteristic of Gramineae.
corpus, according to the tunica-corpus theory, in the shoot apex of Angiospermae that group of cells below the surface layer or layers (i.e. tunica) in which cell divisions take place in various planes; such divisions cause the increase in volume of the shoot apex.
cortex, the tissue region between the vascular cylinder and epidermis of the axis.
cotyledon, the first leaf of the embryo.
crassulae, in tracheids of Gymnospermae transversely-orientated thickenings accompanying the pit-pairs and formed by the intercellular substance and primary wall material.
cross-field, the rectangle formed by the walls of a ray cell and an axial tracheid as seen in a radial section; mainly used in the description of conifer wood.

epidermis, the outermost cell layer of primary tissues of the plant; sometimes comprising more than one layer—*multiseriate epidermis.*
epipetalous stamen, a stamen which is adnated to a petal.
epithem, the tissue between the vein ending and the secretory pore of a hydathode.
ergastic matter, the non-protoplasmic products of metabolic processes of the protoplasm; starch grains, oil droplets, crystals and certain liquids; found in the cytoplasm, vacuoles and cell walls.
eustele, phylogenetically the most advanced type of stele, the vascular tissue of which forms a hollow reticulate cylinder built of collateral or bicollateral vascular bundles.
exalbuminous seed, a seed which is devoid of endosperm when mature.
exarch xylem, in reference to the direction of maturation of the elements in a strand of primary xylem; a strand in which the first-formed elements (the protoxylem) are furthest from the centre of the axis, i.e. the maturation is centripetal.
exine, the outer wall of a mature pollen grain.
exocarp, the outermost layer of the pericarp (fruit wall); also termed *epicarp.*
exodermis, in some roots the outermost layer or layers of cells of the cortex, the structure of which is similar to that of the endodermis, i.e. the cell walls are more or less thickened and contain suberin lamellae. A type of hypodermis.
exogenous, developing from external tissues.

fascicular, being part of or situated in a bundle of vascular tissue.
fibre, an elongated sclerenchymatous cell with tapered ends and with more or less thick secondary walls; the walls may or may not contain lignin and a living protoplast may or may not be retained in the mature fibre.
fibre, gelatinous, a xylem fibre in which the inner layers of the secondary wall have a high capacity to absorb water and to swell.
fibre, libriform, a fibre of the secondary xylem usually with thick walls and simple pits which are generally few in number.
fibre, septate, a fibre which becomes subdivided by thin transverse walls after the secondary wall layers have been formed.
fibre-sclereid, phloem fibres that develop from parenchyma cells of non-functioning phloem.
fibre-tracheid, in the secondary xylem; a transition form between tracheid and libriform fibre.
foraminate, having round pores.
funiculus, the stalk by which the ovule is attached to the placenta.
fusiform, of elongated form with tapered ends.

gametophyte, that plant generation which gives rise to the gametes from which, after fertilization, the sporophyte develops.
gap, branch, in a siphonostele the parenchymatous region in the vascular cylinder above the position where a branch-trace enters a branch.
gap, leaf, in a siphonostele, the parenchymatous region in the vascular cylinder above the position where the leaf-trace enters a leaf.
germination, epigeal, the process of germination in which the cotyledons and epicotyl emerge from the seed as a result of the elongation of the hypocotyl.
germination, hypogeal, the process of germination in which the hypocotyl elongates very little or not at all and the thick cotyledons, which store reserve materials, remain within the testa.
gonophyll, according to the gonophyll theory, a sterile leaf together with an ovule-bearing branch from which it is assumed that the carpel has been derived.
growth, gliding or sliding, that type of growth in which the walls of neighbouring cells slide over one another.

intercellular substance, *see* **middle lamella.**
internode, that part of the stem between two nodes.
interxylary, within and surrounded by xylem tissue.
intine, the inner wall of a mature pollen grain.
intraxylary, on the inner side of the xylem relative to the axis of the plant.
intussusception, cell wall growth as a result of the interpolation of new wall material within the wall already formed.
isobilateral or **isolateral leaf,** a leaf having palisade tissue on both sides of the blade.
isotropic, having equal properties along all axes. Optically—having equal optical properties in all directions.

karyokinesis, the process of nuclear division.
karyolymph, the nuclear sap.
knot, a portion of a dead branch, the wood of which has become heartwood and which is embedded in the developing wood of the stem from which the branch arose.

acuna, (1) an intercellular space; (2) an interruption in the vascular tissue of the central cylinder.
laticifer, a cell or row of cells containing *latex*, a substance specific to such cells.
lenticel, an isolated area in the periderm consisting of suberized or non-suberized cells with numerous intercellular spaces between them.
leucoplastid, a plastid devoid of pigment.
lignin, a mixed polymer containing phenolic derivatives of phenyl propane. Commonly found in secondarily thickened cell walls.
lithocyst, a cell containing a cystolith.
lysigenous, the manner of formation of an intercellular space as a result of the disintegration of cells.

maceration, the artificial separation of the individual cells of a tissue by disintegration of the middle lamella.
macrosclereid, *a somewhat elongated sclereid the secondary wall of which is unequally* thickened. Common in the seeds of Leguminosae where they represent the epidermis of the testa and where they are termed *Malpighian cells.*
Malpighian cell, *see* **macrosclereid.**
mantle, all those outer cell layers of the shoot apex of the Angiospermae which can be distinguished by their layered arrangement from the cells of the inner portion of the shoot apex.
massula, a large group of adherent pollen grains, which participates in the formation of a pollinium.
matrix, a substance in which another substance is deposited or embedded.
median, situated in the middle.
megaspore, the female spore from which the female gametophyte develops; also called *macrospore.*
meristele, one of the bundles of a dictyostele; *see also* **vascular bundle.**
meristem, a tissue which produces cells that undergo differentiation to form mature tissues.
meristem, apical, a meristem situated in the apical region of the shoot or root which, as a result of divisions, gives rise to those cells which form the primary tissues of the shoot or root.
meristem, flank, one of the cyto-histological regions of the shoot apex (see pp.53–57).
meristem, ground, a meristematic tissue which originates in the apical meristem and which produces tissues other than epidermis and vascular tissues.

meristem, intercalary, meristematic tissue derived from the apical meristem and which becomes separated from the apex in the course of develoment of the plant by regions of more or less mature tissues.

meristem, lateral, a meristem which is situated parallel to the circumference of the plant organ in which it occurs.

meristem, plate, a parallel layered meristem in which the planes of cell divisions in each layer are perpendicular to the surface of the organ which is usually a flat one.

meristem, rib, (1) one of the cyto-histological regions of the shoot apex (see p. 53). (2) a meristem characterized by parallel series of cells in which transverse divisions take place.

mesarch xylem, in reference to the direction of maturation of elements in a strand of primary xylem; a strand in which the first-formed elements (the protoxylem) occur in the centre of the strand; i.e. the maturation is both centripetal and centrifugal.

mesocarp, the middle layer of the pericarp (fruit wall).

mesocotyl, often refers to the internode betwen the scutellar node and the coleoptile in the Gramineae.

mesomorphic, having structure characteristic of mesophytes.

mesophyll, the photosynthetic parenchymatous tissue situated between the two epidermal layers of the leaf.

mesophyte, a plant suited to a fairly and continuously moist climate.

metaphloem, that part of the primary phloem which undergoes differentiation after the protophloem.

metaxylem, that part of the primary xylem which undergoes final differentiation after the protoxylem.

micella, the present usage refers to a unit of cellulose in which the molecules are arranged parallel to one another so that the atoms form a crystalline lattice structure.

microfibril, a submicroscopic thread-like constituent of the cell wall; composed in most plants of cellulose molecules.

micropyle, the opening at the free end of the ovule, between the integuments.

microspore, the male spore from which the male gametophyte develops.

microsporocyte, a cell which differentiates into a microspore.

middle lamella, the lamella present between the walls of two adjacent cells.

mitochondrion (plural mitochondria), a very small protoplasmic body in the cytoplasm; contains enzymes involved in respiration.

morphogenesis, the total expression of the morphological phenomena of differentiation and development of tissues and organs.

mother cell, a cell which gives rise to other cells as a result of its division.

multiple (of vessels), referring to the arrangement of vessels as seen in cross-section of the secondary xylem; a group of two or more vessels arranged in radial, oblique or tangential rows.

mycorrhiza, the symbiosis between fungi and the roots of higher plants.

myrosin cell, a cell containing myrosin; present in the vegetative parts and seeds of certain Cruciferae.

nectary, a multicellular glandular structure which secretes a sugary solution. Found in flowers (*floral nectaries*) or on vegetative plant organs (*extrafloral nectaries*).

nexine, the inner layer of the exine.

node, that portion of the stem where a leaf or leaves are attached; anatomically this region cannot be defined accurately.

nucellus, that tissue within the ovule in which the female gametophyte develops.

obturator, an outgrowth of the placenta or stylar canal which brings the transmitting tissue closer to the micropyle.

ontogeny, the process of development of an organism, organ or tissue towards maturation.
osteosclereid, a spool- or bone-shaped sclereid.

paracytic type (of stomata), a specific pattern of arrangement of the guard cells and other epidermal cells adjacent to them (see p. 150).
parenchyma, a ground tissue composed of living cells which may differ in size, shape and wall structure.
parenchyma, apotracheal, axial parenchyma of the secondary xylem, typically independent of the vessels although may occasionally be in contact with them. Divided into the following types according to the distribution as seen in cross-section of the secondary xylem: **banded** or **metatracheal**—concentric uni- or multiseriate bands, arcs or entire rings; **diffuse**—single cells distributed irregularly among fibres; **initial**—bands of parenchyma produced at the beginning of a growth ring; **terminal**—bands of parenchyma produced at the end of a growth ring.
parenchyma, axial, parenchyma of the vertical system of secondary xylem, i.e. parenchyma cells derived from fusiform cambial initials.
parenchyma, paratracheal, axial parenchyma of the secondary xylem associated with the vessels or vascular tracheids. Divided into the following types according to the distribution as seen in cross-section: **aliform**—paratracheal parenchyma which is expanded tangentially in the form of wings; **confluent**—groups of aliform parenchyma which become continuous so as to form irregular tangential or diagonal bands; **scanty**—an incomplete sheath or a few parenchyma cells present around the vessels; **vasicentric**—parenchyma forming an entire sheath of variable width around individual vessels or groups of vessels.
parenchyma, wood, *see* **parenchyma, xylem.**
parenchyma, xylem, parenchyma occurring in the secondary xylem, usually in two systems: (1) axial, and (2) radial (ray parenchyma).
parthenocarpy, the production of fruit without fertilization.
pectic compounds, a group of polymers of galacturonic acid and its derivatives; occurring in three types of compounds—protopectin, pectin and pectic acids. Constituting the most important component of the middle lamella.
perforation (in stele), interruption in the vascular tissue of a siphonostele, other than leaf- or branch-gap; developed as a result of secondary reduction.
perforation plate, that portion of the cell wall of a vessel member which is perforated. The following types of perforation plates are distinguished: (1) *foraminate perforation plate*—a plate with numerous, more or less circular perforations; (2) *reticulate perforation plate*—a plate in which the remnants of the wall between the perforations form a net-like structure; (3) *scalariform perforation plate*—a plate with numerous elongated pores which are arranged parallel one near the other; (4) *simple perforation plate*—a plate having one large perforation.
periblem, *see* **histogen.**
pericarp, the fruit wall.
periclinal, parallel to the surface.
pericycle, that portion of the ground tissue of the vascular cylinder between the conducting tissues and the endodermis.
periderm, the secondary protective tissue which replaces the epidermis; consists of *phellem, phellogen* and *phelloderm.*
perisperm, a nutrient tissue of the seed, similar to the endosperm, but of nucellar origin.
phellogen, the cork cambium; a secondary lateral meristem which produces the phellem and phelloderm.
phloem, the principal tissue responsible for the transport of assimilates in the vascular plants; consists mainly of sieve elements, parenchyma cells, fibres and sclereids.

phloem, interxylary, secondary phloem which occurs within the secondary xylem as is the case in certain Dicotyledoneae.

phloem, intraxylary, primary phloem occurring on the inner side of the primary xylem.

phragmoplast, a fibrous structure which appears during mitotic telophase between the two daughter nuclei; participates in the formation of the cell plate which divides the mother cell into two.

phyllome, a collective term referring to all types of leaves.

phylogeny, the history of a species or a larger taxonomical group from an evolutionary viewpoint.

piliferous cell, *see* **trichoblast.**

pit, a depression in a cell wall with secondary thickening; in such an area only primary wall and middle lamella are present.

pit, bordered, a pit in which the aperture in the secondary wall is small and conceals below it a dome-shaped chamber which is situated above the pit-membrane.

pit cavity, the cavity of a single pit extending from the pit membrane to the aperture bordering the cell lumen.

pitmembrane, the middle lamella and primary wall closing the pit cavity on its outer side.

pit-pair, two complementary pits of neighbouring cells.

pit, vestured, a bordered pit having projections, which may be simple or branched, on that part of the secondary wall which forms the border of the pit chamber or the pit aperture; found in certain Dicotyledoneae.

pith, the ground tissue in the centre of the stem and root.

pitting, the type and arrangement of pits in the cell wall.

placenta, the region of attachment of the ovules to the carpel.

placentation, the position of the placenta in the ovary.

plasmalemma, the membrane on the outer surface of the cytoplasm; adjacent to cell wall. Also known as *ectoplast.*

plasmodesma, a thin, cytoplasmic strand which passes through a pore in the cell wall, and which usually connects the protoplasts of two adjacent cells.

plastid, a protoplasmic body separated from the cytoplasm by a membrane; fulfilling a definite function.

plastochron, that period of time between the commencement of two successive and repetitive phenomena, for example, between the initiation of two successive leaf primordia.

plectostele, a protostele in which the xylem is arranged in longitudinal plates which may be interconnected.

plerome, *see* **histogen.**

plumule, the bud or shoot apex of the embryo.

pneumatode, in a velamen, a group of cells with very dense spiral wall thickenings; enables gas exchange when the root is saturated with moisture.

pneumatophore, an aerial, negatively geotropic root projection serving for gas exchange; produced in swampy habitats.

pollen tube, an elongated projection, covered only by intine, of the vegetative cell of a pollen grain.

pollinium, the entire pollen grain complement of a single pollen sac, when the grains adhere together to form one mass.

polyarch, the primary xylem of root in which the number of protoxylem strands is large (usually more than five).

polyderm, a special type of protective tissue composed of alternating bands of endodermis-like cells and non-suberized parenchyma cells.

polyembryony, the presence of more than one embryo in an ovule.

primary pit-field, a thin portion of the primary wall in which the pores, through which plasmodesmata pass, are concentrated.

primordium, an organ, cell or organized group of cells in the earliest stage of differentiation.

scutellum, a part of the embryo of the Gramineae; considered to be homologous to a cotyledon; serves as an organ which transfers nutrients from the endosperm to other parts of the germinating embryo.

separation layer, that layer in the abscission zone the cells of which disintegrate or separate and so cause the abscission of the organ concerned or part of it, e.g., leaf, branch, fruit, fruit valves, etc.

sexine, the outer layer of the exine.

shoot, the stem and its appendages.

sieve area, an area on the wall of a sieve element which appears as a depression and which contains pores lined with callose.

sieve cell, a sieve element in which the sieve areas have undergone relatively little differentiation, i.e. they are of more or less uniform structure and have narrow pores and connecting strands.

sieve element, that type of phloem element which takes part in the transport of assimilates. Classified into two types—*sieve cell* and *sieve-tube member*.

sieve plate, that part of the cell wall of a sieve element which contains one or more highly specialized sieve areas. Characteristic of the Angiospermae.

sieve tube, a series of sieve-tube members which are arranged end to end and which are connected through their sieve plates.

sieve-tube member, one of the cells of which a sieve tube is comprised.

silica cell, a short epidermal cell filled with silica as occurs in the epidermis of the Gramineae.

siphonostele, a stele in which the vascular tissue comprises a hollow cylinder, i.e. in which the central portion is occupied by pith.

siphonostele, amphiphloic, a siphonostele in which the phloem surrounds the xylem both externally and internally.

siphonostele, ectophloic, a siphonostele in which the phloem surrounds the xylem on the outside only.

soft wood, a common name for wood of the Gymnospermae, in particular the Coniferae.

solenostele, an amphiphloic siphonostele in which the successive leaf-gaps are considerably distant one from the other.

specialization, the changes during the course of evolution in structure of a cell, tissue, organ or entire plant, which enable it to carry out a certain function more efficiently.

sporophyte, that plant generation which produces spores from which the gametophyte develops.

starch sheath, referring to the innermost layer of the cortex, when its cells are characterized by presence of a large, more or less constant quantity of starch; homologous with the endodermis.

stele, that portion of the plant axis which comprises the vascular system and its associated ground tissue, i.e. pericycle, interfascicular regions and pith.

stele, polycyclic, a stele consisting of two or more concentric cylinders of vascular tissue.

stereome, a collective physiological term for all the supporting tissues in the plant, i.e. sclerenchyma and collenchyma.

strophiole, a growth on the funiculus and/or seed.

suberization, the deposition of suberin in cell walls.

subsidiary cell, *see* **accessory cell.**

succulent, fleshy, juicy.

supporting tissue, *see* **tissue, mechanical.**

surface layer or **surface meristem,** one of the cyto-histological zones of the Gymnospermae shoot apex.

suspensor, that part of the embryo which connects its main part to the basal cell.

syncarpy, that condition in a flower and ovary where the carpels are fused.

synergids, the cells present alongside the egg cell in a mature embryo sac.

procambium, a primary meristem which undergoes differentiation to form the primary vascular tissues.
pro-embryo, the embryo in the earliest stages of development.
promeristem, the initials and their immediate derivatives in the apical meristem.
prophyll, one of the first leaves of a lateral branch.
proplastid, a plastid in the earliest stages of development, a primordial plastid.
protoderm, the meristem of the epidermis.
protophloem, the first-formed elements of the primary phloem.
protostele, the simplest type of stele which comprises a solid core of xylem surrounded by phloem.
protostele, medulated, according to the terminology of some authors, an ectophloic siphonostele without leaf-gaps; occurs in Pteridophyta.
protoxylem, the first-formed elements of the primary xylem.
provascular bundle, a procambium strand.
pseudocarp, a fruit in which floral organs other than the carpels participate in the formation of its wall.
pulvinus, the swelling at the base of a leaf petiole or of a petiolule of a leaflet.

raphe, a ridge along the seed formed by that part of the funiculus which was fused to the ovule.
raphide, a needle-shaped crystal usually occurring in dense bundles.
ray, phloem, that part of the vascular ray which passes through the secondary phloem.
ray, pith, an interfascicular region in a stem.
ray, vascular, a strip of tissue running radially through the secondary xylem and phloem; formed by the cambium.
ray, xylem, that part of the vascular ray which passes through the secondary xylem.
replum, the ridge surrounding the siliqua of the Cruciferae which remains attached to the false septum, as a frame, on the dehiscence of the fruit.
rhytidome, that part of the bark comprising the periderm and tissues external to it which are cut off by it. Also called *outer bark*.
ribosome, a minute protoplasmic body in the cytoplasm playing an important role in protein synthesis.
ring-porous wood, *see* **wood.**
rod cell, *see* **macrosclereid.**
root-cap, a thimble-shaped structure which covers the root apex.
root, contractile, a special root which has the ability to contract and thus bring the developing renewal buds to a definite position in relation to the soil surface.
root hair, a type of trichome developing on the epidermis of roots; absorbs solutions from the soil.

sapwood or **alburnum,** that portion of the wood that in the living tree and shrub contains living cells and reserve materials.
scalariform, the parallel arrangement, one near the other, of elongated structures in the cell wall of an element.
schizogenous, the manner of formation of intercellular spaces by the separation of cells along their middle lamellae.
schizo-lysigenous, the manner of formation of intercellular spaces by both cell separation along their middle lamellae and cell disintegration.
sclereid, a sclerenchymatous cell of various shape, but usually not much elongated; has thick, lignified secondary wall which often contains many pits.
sclerenchyma, a supporting tissue composed of fibres and/or sclereids.
sclerification, the process of changing into sclerenchyma by the formation of secondary walls.

tapetum, the innermost layer of the pollen sac wall; the contents of its cells are absorbed by the pollen grains during their development.

tapetum, amoeboid, tapetum in which the protoplasts of its cells penetrate between the pollen mother cells and developing pollen grains; **glandular,** tapetum in which the cells remain in their original position until their disintegration.

telome, the ultimate terminal portion of a dichotomously branching axis bearing a sporangium (fertile telome) or lacking a sporangium (sterile telome). According to the *telome theory* the most primitive vascular plants were composed entirely of telome systems.

testa, the seed coat.

tetrarch, the primary xylem of root in which the number of protoxylem strands is four.

tissue, complementary, *see* **cells, complementary.**

tissue, conjunctive, (1) a special type of parenchyma associated with included phloem in Dicotyledoneae with anomalous thickening; (2) the parenchyma present between the secondary vascular bundles of Monocotyledoneae with secondary thickening.

tissue element, each individual cell of a tissue.

tissue, expansion, an intercalary tissue in the outer portion of the inner bark formed mainly by the phloem rays; accommodates the expansion in circumference.

tissue, ground, all the mature plant tissues except the epidermis, periderm and vascular tissues.

tissue, mature, a tissue which has undergone differentiation.

tissue, mechanical, a tissue comprised of cells, the walls of which are more or less thickened; such tissues give support to the plant body. Also referred to as *supporting tissues.*

tissue, proliferation, a tissue which develops from phloem parenchyma in the outer portion of the inner bark accomodating the expansion in circumference.

tissue, transfusion, that tissue which, in the leaves of the Gymnospermae, surrounds or is associated in some other way with the vascular bundles. Comprised of dead tracheids and living parenchyma cells.

tissue, transmitting, a tissue in the style similar to the tissue of the stigma in both structure and physiological properties; connects the stigma and the inside of the ovary.

tonoplast, the cytoplasmic membrane which borders the vacuole.

torus, the thickened central portion of the pit membrane in a bordered pit.

trabecula, a rod-like projection of the cell wall which crosses the cell lumen, usually in a radial direction.

trace, branch, that part of a vascular bundle in the stem extending from the position where it joins the vascular system of the branch to where it joins the vascular system of the main stem.

trace, leaf, that part of a vascular bundle in the stem from the position where it enters the leaf to where it joins the vascular system of the stem.

trachea, *see* **vessel.**

tracheary element, that type of xylem element which takes part in water transport. Classified into two types—*tracheid* and *vessel member.*

tracheid, a tracheary element of the xylem, which unlike the vessel member, is not perforated.

triarch, the primary xylem of root in which the number of protoxylem strands is three.

trichoblast, a specialized cell in the root epidermis which gives rise to a root hair.

trichome, an epidermal appendage; may be of various shapes, structures, size and function; includes hairs, scales, etc.

tunica, the outermost layer or layers in the apical shoot meristem of the Angiospermae in which the plane of division is almost entirely anticlinal.

tylosis, *an outgrowth of a ray cell or of an axial parenchyma cell into the lumen of a* vessel; such outgrowths partially or completely block the vessels.

tylosoid, a proliferation of an epithelial cell into an intercellular cavity such as resin or gum duct.

unifacial leaf, a leaf in which the structure of both sides is alike and in which each side forms a mirror-image of the other side. Ontogenetically, a leaf which develops from a centre of growth situated on one of the sides of a leaf primordium.

vacuolation, the shape, amount and size of the vacuome. Also the process of forming vacuoles.
vacuole, a cavity in the cytoplasm containing an aqueous solution, the cell sap.
vacuome, the collective term for all the vacuoles of a single cell.
vascular, an adjective referring to the xylem or phloem or both.
vascular bundle, a strand of conducting tissue. The following types of vascular bundles are recognized: (1) *bicollateral vascular bundle*—vascular bundle in which phloem is present both on the outside and inside of the xylem; (2) *collateral vascular bundle*—vascular bundle in which phloem is present on one side of the xylem only, commonly external to it; (3) *concentric vascular bundle*—vascular bundle in which the phloem surrounds the xylem (i.e. amphicribral) or the xylem surrounds the phloem (i.e. amphivasal).
vein, a strand of vascular tissue in a flat organ, such as a leaf.
velamen, the multiseriate epidermis present on the aerial roots of some ropical epiphytic species of the Orchidaceae and Araceae; also present on some terrestrial roots.
venation, the arrangement of the veins in the leaf blade.
vessel, a series of vessel members joined end to end by their perforated end walls. Also termed *trachea.*
vessel member, a tracheary element, one of the cells of which a vessel is comprised.

wall, general, the gelatinous wall which at first surrounds the pollen mother cell and then later the developing tetrad.
wall layer, terminal, *see* **wall layer, tertiary.**
wall layer, tertiary, according to some authors, a layer present on the inside of the inner layer of the secondary wall.
wall, special, the first wall formed which separates each of the pollen grains in the tetrad.
wart structure, small granules occurring on the inner surface of the secondary wall of tracheids, fibres and vessels.
wood, compression, the reaction wood of the Coniferae, formed on the lower side of bent or leaning trunks and branches.
wood, diffuse-porous, the secondary xylem of a single growth ring in which the vessels are more or less uniformly distributed or in which the diameter of vessels alters only slightly across the growth ring.
wood, reaction, the secondary xylem with special structure, produced in those parts of trunks and branches which lean or are bent; apparently tends to return these organs to their original position. *Tension wood* in the Dicotyledonae; *compression wood* in the Coniferae.
wood, ring-porous, secondary xylem of a single growth ring in which the vessels produced at the beginning of a growth season are significantly larger than those produced at the end of the season.
wood, tension, the reaction wood of the Dicotyledoneae formed on the upper side of leaning or bent trunks and branches.
woody, an entire plant or a plant organ with well developed secondary xylem.

xeromorphic, having structure typical of xerophytes.
xerophyte, a plant adapted to arid habitats.
xylem, the tissue mainly responsible for conduction of water in vascular plants; characterized by the presence of tracheary elements. Xylem, especially secondary xylem, may also serve as a supporting tissue.

AUTHOR INDEX

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SUBJECT INDEX

Numbers in *italics* indicate that emphasis is placed on the subject. Numbers in **bold type** indicate that the subject is cited in a figure or in a legend to a figure