AN INTRODUCTION TO PLANT ANATOMY

BY

ARTHUR J. EAMES

Professor of Botany, Cornell University

AND

LAURENCE H. MACDANIELS

Professor of Horticulture, Cornell University

She EDITION

McGRAW-HILL BOOK COMPANY, INC.

NEW YORK AND LONDON

1947

PREFACE TO THE SECOND EDITION

In the second edition of this textbook the authors have maintained the viewpoint and the aims of the first edition: a textbook, introductory in level, that will serve primarily for classroom use, and only secondarily as a reference text. They have been mindful of the request that the new edition present greater amounts of detailed description and that it cover aspects of the field not treated in the first edition—that it include, for example, "full details of meristem development" and a discussion of the structure of chimeras and their significance. The inclusion of such additions is obviously impossible in a book of this type and size.

Since the preparation of the first edition, there has been marked progress in our knowledge of certain fields of plant anatomy, especially cell-wall origin, development, and structure; meristems; phloem; leaf development; abscission; flower and fruit structure. The authors have incorporated into the new edition as much from this material as in their opinion properly belongs in this book. These additions have increased the length of most of the chapters, and in an effort to keep the book at approximately its original size, Chap. XV—A Sketch of the History of Plant Anatomy—has been omitted because, although of general interest, it is not essential to the student in gaining a working knowledge of plant anatomy.

A few changes have been made in the terminology used in the first edition. Some changes have been made because the structure of certain cells and tissues, such as the phloem, is more fully understood today than in 1925; other changes have been made so that the terminology of the textbook conforms with a glossary of terms used in describing wood, adopted by the International Association of Wood Anatomists.

The authors wish to acknowledge the help of Dr. Antoinette M. Wilkinson and Dr. H. W. Blaser, who were especially helpful in the preparation and reading of the manuscript. They are also greatly indebted to Mrs. Rita B. Eames for her assistance with the preparation and improvement of the illustrations and her supervision of the manuscript. The authors also wish to thank W. R. Fisher for his interest and cooperation in making many of the photographs in this book.

ARTHUR J. EAMES LAURENCE H. MACDANIELS

ITHACA, N.Y., July, 1947.

PREFACE TO THE FIRST EDITION

In presenting this book the authors hope to fill a need for a textbook in plant anatomy of a type at present not available—a need which they, as teachers in this field, have keenly felt. Not only, however, in their opinion, is there need for a book for class study and guidance, but also for one which shall serve as a reference text for workers in fields of applied botany, and for teachers and students in other fields of pure botany. A double purpose, therefore, has been kept in mind in the preparation of the book. In the treatment of the subject matter, however, emphasis has been placed on adaptability to classroom use from the standpoint of the student beginning anatomical study. Thus, the book is, first of all, a textbook in the elements of plant anatomy—an introduction to the field. It presupposes an acquaintance only with the fundamental structure and activities of plants—an acquaintance such as is ordinarily obtained from a first course in botany.

Though the book is thus introductory in nature, it is believed to embody a fairly comprehensive treatment of the fundamental facts and aspects of anatomy—to be, in fact, so inclusive as to provide a working basis for independent study. Yet it does not lay claim to the exposition, in detail, of the known facts and the theories concerning any structural features. So great is the number of recorded facts, and so confused is the terminology of anatomy, that a treatise approaching completeness in the presentation thereof would not be usable as a textbook. Further, the anatomy of vascular plants, especially that of the angiosperms is, in detail and in some broader features, still largely unknown. It is thus obviously impossible to present data covering the facts and structural features which will be met by the student in later work. It is, further, the firm opinion of the authors that the student of anatomy should not learn facts primarily, but should be taught self-reliance in the study of plant structure through training in power of observation and interpreta-Therefore, the book is not a compendium of facts.

Training which results in independence in the study of anatomy is, of course, secured only by laboratory practice. On such practice the authors believe emphasis must be placed, and not on lectures, text study, nor, in the beginning, on reading. For laboratory teaching the present book should provide a background of facts, terms, history, etc.; it may, indeed, be used, in part, as a laboratory guide. The sequence of subjects adopted is that which in the experience of the authors has been

found most satisfactory in laboratory work. Such material as is specifically mentioned, or is used for illustration, suggests only in a general way the range and the amount of material that may be used in a first course in plant anatomy. It is not necessary, nor is it even desirable, that the same plants be used in the classroom. Any available material may be used, and, by comparison with the descriptions and illustrations of the text, the teaching can be made more effective. The authors in their own classes use considerable material, sufficient to cover so far as possible the range and type of variation in each structure. An acquaintance with variation is thus acquired by the student, and a power of interpretation is given by practice with many examples, so that he is enabled thereafter to interpret wholly new material.

As a reference book, the synoptical treatment of the more important facts, usage of terms, present status of opinion, etc. should render the book generally useful. More detailed information may be obtained, of course, from the larger reference works, though often it is only to be found in papers and articles of limited scope. A certain small amount of material embodied in the book represents the result of unpublished research and observation on the part of the authors, or represents their personal opinions.

Except for an occasional mention of lower forms, the structure of vascular plants only is considered, since the histological structure of the thallophytes is usually not complex. Where it is, the method of study and the terms applied to cells and tissues in higher plants may generally be used. In the selection of forms for illustration there have been chosen, so far as available material has permitted, well-known or economically important plants.

The viewpoint of the treatment is fundamentally that of descriptive morphology, that is, of existent form and structure. Physiological anatomy regards form but little; yet an understanding of form and of structural relationship must precede all valuable anatomical study. The physiological aspects and the practical bearing of the subject matter are discussed briefly, and incidentally to the general treatment. Comparative morphology is made use of whenever an understanding of phylogenetic development helps to make structural complexity clear. A textbook written on the basis of descriptive morphology the authors believe to be most generally useful. For students going beyond the introductory steps in anatomy, however—either into the various fields of applied subjects, such as pathology and horticulture, or into any field of the pure science—a complete understanding of morphological modification and variation can be obtained only through the consideration of the phylogenetic history of the structure in question.

The book does not pretend to present the historical development of our knowledge of the field, or of any phase or part thereof; nor are the contributions of prominent students brought out as the work of individuals. The present status of knowledge and opinion is made the first aspect of treatment; secondarily, other viewpoints are considered. Chapter XV, however, outlines the history of the subject, and deals briefly with the contributions of some of the earlier prominent students of anatomy. This historical sketch is placed at the end of the book, since the beginning student may best make use of it only when he has acquired an understanding of the subject matter.

Owing to the state of confusion which exists in the terminology of anatomy, it has in many cases been necessary to evaluate the different uses of terms. For use in the book, those terms have been accepted which seem best on a basis first of morphological usefulness and secondly, of priority; in a few instances the history and the use of a term are briefly discussed.

Since the book is primarily an elementary text and not a text for research reference nor for the use of advanced students, the bibliography has been kept at a minimum. After each chapter there are listed a few of the more recent and more important books and articles—and sometimes those valuable for their own bibliographies—dealing with the subjects discussed in that chapter. By reference to these, students may obtain longer lists. Such a method of citation naturally often excludes the older, "classic" treatments. To the first chapter is appended a list of texts which are generally useful for some or for many phases of the subject. Reference to these texts is not repeated after the various chapters, except where the book in question deals particularly with the subject matter of a chapter.

The common names of plants have for the most part been omitted from the text. They may be sought in the index, as such, and also under the generic names with which they are associated.

In present-day botany, the terms "anatomy" and "histology" are often loosely used. To many botanists the study of the internal structure of plants is unfortunately known as histology. This is doubtless due in part to the fact that histology deals with the structure of cells and tissues—internal structure meaning this and little more—and in part to the fact that the grosser internal structures, such as steles and traces, have been consistently neglected in courses in "histology." The study of these features of grosser internal structure, and sometimes of those of external make-up also, have been looked upon as "anatomy." Anatomy, however, deals with the structure of organisms, structure both gross and minute, external and internal. Histology, which deals with the minute

structure of organisms, is, therefore, a part of the broader field of anatomy. An understanding of the structure of a plant obviously cannot be obtained from the study of minute features alone. Thus, a treatment such as is here presented is anatomical rather than histological, and the book is, therefore, a text in Plant Anatomy.

In so far as the treatment in its histological aspects deals with the structure of cells—especially wherever the protoplast is concerned—it enters the field of cytology; and cytology in recent years has become an independent division of biological science. Cytological aspects of anatomy, therefore, need not be considered, and have been omitted from the discussion except in so far as they are essential to histological study. An arbitrary limit has necessarily been set to the description of the cell. The protoplast is very briefly discussed, except for the paragraphs on plasmodesma, plastids, and cell inclusions; nuclear division is omitted since it is ordinarily taught in first courses in botany, and again in greater detail in cytology. The wall, however, which, aside from aspects of origin and early development, is usually considered by cytologists as a histological feature, is more fully treated.

The illustrations have in large part been made directly from the material itself. The explanation of the figures is placed chiefly in the legends. With a few exceptions, the drawings are the work of the authors themselves and of Mrs. Rita Ballard Eames to whom the authors are greatly indebted for invaluable assistance and suggestions. The helpful criticism of their colleagues the authors also desire to acknowledge.

ARTHUR J. EAMES
LAURENCE H. MACDANIELS

ITHACA, N.Y., July, 1925.

AN INTRODUCTION TO PLANT ANATOMY

COPYRIGHT, 1925, 1947, BY THE
McGraw-Hill Book Company, Inc.
Copyright renewed 1953, by Arthur J. Eames and Laurence H. McDaniels
PRINTED IN THE UNITED STATES OF AMERICA

All rights reserved. This book, or parts thereof, may notbe reproduced in any form without permission of the publishers.

VII

CONTENTS

Preface to the Second Edition	vii
Preface to the First Edition	ix
INTRODUCTORY	
Chapter I	
General Structure of the Plant Body—An Outline Fundamental parts—The axis—The stele—Primary and secondary growth—Constitution of the plant body—Methods of study—General references for plant anatomy.	1
$GENERAL\ HISTOLOGY$	
Chapter II	
The Cell	6
Chapter III	
Meristematic and permanent cells and tissues—Classification based on: stage or method of development, history of initiating cells, position in plant body, function—Theories of structural development and differentiation: apical cell theory, histogen theory, tunica-corpus theory—Types of stem apices—Discussion of tunica-corpus theory—The floral apex—The root apex—Types of root-tip development—References for Chap. III.	60

CONTENTS

${\it Chapter\ IV}$

Tissues based on stage of development: meristematic, permanent—Tissues based on kind of constituent cells: simple (parenchyma, collenchyma, sclerenchyma); the important complex tissues (xylem, phloem, "transfusion tissue")—Tissue systems—Secretory tissue—References for Chap. IV.	81
THE PRIMARY BODY	
Chapter V	
Primary tissues and tissue systems—Ontogeny of the axis—Primary vascular tissue: procambium, protophloem and protoxylem, primary phloem, primary xylem, arrangement of cells in primary vascular tissues, primary xylem types, types of vascular bundles—The primary vascular skeleton: the stele, stelar types, leaf traces, branch traces, leaf and branch gaps, the dissection of the vascular cylinder by reduction, general structure of the primary vascular cylinder—The pith: structure, the medullary sheath, of roots, duration—The pericycle—The endodermis: occurrence and position, function as related to structure—The cortex—The epidermis: ontogeny and duration, function, root hairs, the stoma, hairs—References for Chap. V.	123
THE SECONDARY BODY	
Chapter VI	
The Origin and Development of the Secondary Body and Its Relation to the Primary Body. The Cambium	175

bium—Structure of cambium: size of cells, structure of cells, cell division—Gliding and intrusive growth of cambial cells and cambial derivatives—Ontogeny of secondary vascular tissues—

Time of cambial activity—Burial of branch bases—Cambium growth about wounds—Cambium in budding and grafting—Cambium in monocotyledons—References for Chap. VI.	
Chapter VII	
Gross structure: xylem rays, annual rings, growth rings, early and late wood, false annual rings, ring-porous and diffuse-porous wood—Histological structure: cell types and cell arrangement, wood-parenchyma distribution, structure of gymnosperm wood, structure of angiosperm wood, xylem rays, ray tracheids, marginal ray cells of angiosperms, tyloses—Sapwood and heartwood—Relation of microscopic structure to properties and uses of wood: weight, strength, durability, other properties—Penetrability by preservatives—Grain of wood—Compression wood—Pith-ray flecks—Gummosis—References for Chap. VII.	204
Chapter VIII	
Secondary Phloem	231
Chapter IX	
PERIDERM AND ABSCISSION	248
· THE ORGANS	
Chapter X	
The Root	277

mary vascular tissues—Secondary growth—Formation of lateral roots—Adventitious roots—Periderm—References for Chap. X.

Chapter XI

Chapter XII

Morphology—Arrangement—Ontogeny—Duration of leaf development—Vascular tissue: development, orientation, xylem and phloem elements, bundle ends—Bundle sheath—Mechanical support—Mesophyll—Epidermis—Distribution of stomata—The monocotyledonous leaf—The grass leaf: sclerenchyma, bundle sheaths, mesophyll, epidermis, arrangement of stomata—Persistence of leaves—References for Chap. XII.

Chapter XIII

THE FRUIT. Morphology—Ontogeny—Structure—Vascular skeleton—Epidermis—Periderm—Fleshy fruits—Dry fruits—The placenta—Accessory fruit parts—Dehiscence.

THE SEED. Seed coats: morphology, histological structure, vascular bundles—Embryo and endosperm—References for Chap. XIII: flower, fruit, seed.

CONTENTS

xvii

ECOLOGY

Chapter XIV

Ecological Anatomy	380
chyma, reduction of vascular and absorbing tissues—Shade leaves—Parasites—"Saprophytes"—References for Chap. XIV.	
Lypey	207

CHAPTER I

GENERAL STRUCTURE OF THE PLANT BODY-AN OUTLINE

Among vascular plants there is very great diversity in size, form, and structure; yet, underlying the variations in form and the complexities in structure in the plant body, there is a simple, uniform, structural plan. The body consists fundamentally of a cylindrical *axis* which bears lateral appendages. The more or less free branching of the axis and the variety and complexity of the appendages, however, often conceal this simplicity of plan.

Fundamental Parts of the Plant Body.—The axis, though a continuous structure, consists of two parts, different structurally and physiologically, and clearly morphologically distinct: that portion which is normally aerial is known as the stem, and that portion which is subterranean is called the root (Fig. 1). The appendages are of three ranks. into which pass strands of vascular tissue may be said to be of the first rank, and are known as leaves. Appendages of this type are characteristic of the stem and do not occur on the root. They are arranged in a definite manner, and bear an intimate structural relation to the skeleton of the axis. The leaf may be looked upon from the standpoint of the present treatment as a lateral expansion of the stem, continuous with it, in the formation of which all fundamental parts of the stem are concerned. In the appendages of the second rank only the outermost lavers of the stem, the cortex and the epidermis, are usually present. These are known as emergences; the prickles of the rose are a familiar example. In appendages of the third rank, projections of the outermost layer of cells only are present; these form hairs. Emergences and hairs occur on both axis and leaves, usually without definite arrangement.

The Axis.—The axis itself consists of a central core with a surrounding, ensheathing layer. This core serves chiefly the important functions of conduction and support; it contains the vascular tissue and the larger part of all the supporting and conducting cells of the mature axis. Because of its shape and its position in the axis, this central unit mass is known as the central cylinder, or stele (Fig. 2). The surrounding layer, which serves for protection, support, storage, and for other purposes, is the cortex; the outermost layer of cells is the epidermis.

The Stele.—Primarily, the stele is composed of vascular tissue of two types: that which conducts water and other substances absorbed

from the soil, the *xylem*; and that which carries the food (and possibly mineral nutrients), the *phloem*. Xylem and phloem nearly always occur together, usually side by side radially, the phloem outermost (Fig. 2). These tissues together may form a solid rod, a hollow cylinder, a sheath

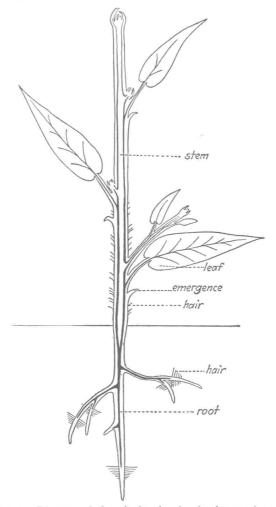


Fig. 1.—Diagram of plant body, showing fundamental parts.

of more or less symmetrically placed strands (Fig. 66), or a group of scattered strands (each consisting of xylem and phloem). Where the arrangement of the vascular tissues is such that they enclose tissue of a different type, usually soft and loose, a central portion, the *pith*, is set off. Outside the external conducting cells and forming the outermost

part of the stele are a few layers of nonconducting cells, the *pericycle*. The pericycle is usually limited externally by a definite uniseriate sheet of cells of peculiar structure, the *endodermis*. The vascular core is thus ensheathed by the pericycle in a way similar to that in which the stele is enveloped by the cortex.

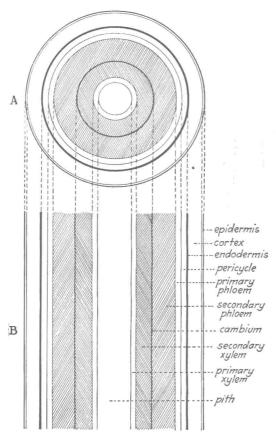


Fig. 2.—Diagram showing structure of axis. A, transverse section; B, longitudinal section.

Primary and Secondary Growth.—An axis complete in all the structural features above mentioned and with complete appendages is built up by growth at the growing points, situated at the tips of the axis. This first-formed body is known as the *primary body*, since it is built up by first, or *primary*, *growth*. Its tissues are, for the same reason, known as *primary tissues*; for example, the first-formed xylem is called *primary xylem*. In many vascular plants the primary body is reinforced by a different sort of growth, which because it begins later and adds to

the original primary tissues is called *secondary growth*. The tissues thus formed are termed *secondary tissues*. Secondary growth does not usually form new types of cells, but merely increases the bulk of the plant, especially of the vascular tissues, providing new conducting cells and additional support and protection. It does not fundamentally change the structure of the primary body. Primary growth increases the length of the axis, laying down its branching system and adding its appendages; that is, it builds up the new, or young, parts of the plant body. After

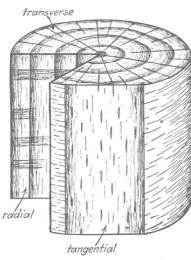


Fig. 3.—Diagrammatic sketch of a cylinder of wood, to show transverse, radial, and tangential planes of section.

the parts thus formed have attained full size, additional increase in diameter is secured only by secondary growth.

The secondary vascular tissues are formed by a specialized growing layer, the cambium, which arises between the primary xylem and the primary phloem, and lays down new xylem and phloem adjacent to these. The secondary masses of xylem and phloem lie, therefore, entirely within the central cylinder and between the primary phloem and primary xylem. The newly formed xylem cloaks and ultimately completely surrounds the primary xylem and the pith, not changing the primary structure within, but burying it intact. The pri-

mary phloem and all other tissues outside the cambium are forced outward by secondary growth and may be ultimately more or less distorted or destroyed. The primary growth of a given region is completed in a relatively brief period, whereas secondary growth continues for a longer time, and in perennial axes may persist indefinitely.

Constitution of the Plant Body.—The root, stem, and leaves of a plant constitute its *organs*. These perform distinct, general functions for which they are adapted by the kinds, proportion, and arrangement of the *tissues* of which they are composed. The tissues have more restricted functions, which are determined by the kinds of *cells* that constitute them. The plant body thus consists of cells that, aggregated, form tissues; these grouped together, form organs.

Methods of Studying the Anatomy of the Plant.—The principal methods of studying the minute structure of the plant body are by means of thin sections of plant material and macerations in which the individual

cells are freed from one another. Moreover, for adequate comprehension of the complex structure of most parts of the plant, study of sections cut in more than one plane is necessary. For the axis—a cylindrical structure—three planes, each at right angles to the other two, are most useful. One plane is transverse to the long axis; the others are parallel with the long axis, that is, longitudinal. Of the two longitudinal planes, that dividing the cylinder radially is the radial plane, and that at right angles to the radial plane is the tangential plane (Fig. 3). Sections cut in these planes are known as transverse (or cross), radial, and tangential sections respectively.

General References for Use with All Chapters

BONNIER, G., and LECLERC DU SABLON: "Cours de botanique," Paris, 1905.

DE BARY, A.: "Comparative Anatomy of the Phanerogams and Ferns," Engl. transl., Oxford, 1884.

Bower, F. O.: "Size and Form in Plants (with Special References to the Primary Conducting Tracts)," London, 1930.

Committee on Nomenclature, International Association of Wood Anatomists: Glossary of terms used in describing woods, *Trop. Woods*, **36**, Dec., 1933.

FOSTER, A. S.: "Practical Plant Anatomy," New York, 1942.

Guilliermond, A.: "The Cytoplasm of the Plant Cell," Engl. transl. by L. R. Atkinson, Waltham, Mass., 1941.

HABERLANDT, G.: "Physiological Plant Anatomy," Engl. transl. of 4th Germ. ed., London, 1914.

----: "Physiologische Pflanzenanatomie," 5th Germ. ed., Leipzig, 1918.

HAYWARD, H. E.: "The Structure of Economic Plants," New York, 1938.

JEFFREY, E. C.: "The Anatomy of Woody Plants," Chicago, 1917.

Sharp, L. W.: "Fundamentals of Cytology," New York, 1943.

Sifton, H. B.: Developmental morphology of vascular plants, New Phyt., 43, 87–129, 1944.

Solereder, H.: "Systematic Anatomy of the Dicotyledons," Engl. transl., Oxford, 1908.

——, and F. J. Meyer: "Systematische Anatomie der Monocotyledonen," Berlin. I, 1928; III, 1929; IV, 1930; VI, 1933.

STRASBURGER, E.: "Histologische Beiträge," III, Jena, 1891.

Troll, W.: "Vergleichende Morphologie der höheren Pflanzen. I. Vegetatsionsorgane." Lief. 1. Berlin, 1935.

TSCHIRCH, A.: "Angewandte Pflanzenanatomie," Vienna, 1889.

Van Tieghem, P.: "Traité de botanique," Paris, 1891.