COMPARATIVE MORPHOLOGY OF VASCULAR PLANTS

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BY ADRIANCE S. FOSTER
University of California, Berkeley

AND ERNEST M. GIFFORD, Jr.
University of California, Davis

Drawings by EVAN L. GILLESPIE

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Preface

Preparing a modern textbook that will adequately and interestingly display to both student and teacher the present state of knowledge of the comparative morphology of vascular plants is indeed a formidable and challenging task. The divergence in opinion as to how the vast body of morphological knowledge accumulated during the past century should be presented in university or college courses is clearly reflected in certain recent texts. Some authors restrict themselves to a very detailed treatment of the structure, reproduction, and evolution of lower vascular plants. Others present a more elementary treatment of vascular plants as a whole, together with a survey of the entire plant kingdom. Because there are such wide variations in teaching methods and in the content of botanical curricula in colleges and universities, each type of book undoubtedly serves a purpose and has value. But we believe that today there is a great need for a textbook, which, in addition to providing a purely factual description of all the main groups of vascular plants, will also display clearly the procedures, general principles, and objectives of comparative morphology. This volume has been written and organized from this point of view. We hope that our text will in some measure orient and vitalize the teaching of plant morphology and that it will also emphasize the important relationships between morphology, taxonomy, and experimental morphogenesis.

The present volume has grown from teaching experience, and it is primarily intended to function as the text for an advanced one-semester course in plant morphology—a course such as that taught by the authors for many years at the University of California consisting of two lectures and six hours of laboratory work per week for a period of 15 weeks. However, this book is, in our judgment, also sufficiently comprehensive for use in a year course at either the senior or graduate level.

Because of the excessive fragmentation which all the classical fields of botany are now experiencing, it seems essential at the outset to discuss in broad terms the nature and objectives of the science of plant morphology. This we have attempted to do in the opening chapter, which also includes pertinent discussions of the concept of homology in plants and of the major lines of evidence upon which morphological interpretations are based. We believe the student requires this type of introduction—frequently omitted from modern texts—before he can be expected to pursue with any motivation the inevitable details of comparative morphology.

The student of plant morphology may, as can easily happen in any science, miss the forest because of the trees. To avoid this common difficulty insofar as possible, a series of orientation chapters (Chapters 2 through 6) are introduced before presentation of the comparative morphology of the several groups of vascular plants. In these chapters we have attempted to summarize and to appraise (1) the salient morphological features and common plan of the reproductive cycle in vascular plants, (2) the general organography and anatomy of the vegetative sporophyte, and (3) the structure and development of sporangia, gametangia, and embryos. The essential subject matter of these chapters could serve as the basis for the early lectures in a course in plant morphology. But we hope also that the frequent cross-referencing between these introductory chapters and later portions of the book may more closely relate *morphological principles* to the discussions of the structure and reproduction in specific types of vascular plants.

For reasons that are briefly explained in Chapter 2, we have adopted the designation "Tracheophyta" as representing the vascular plant "division" of the plant kingdom, and under this division we recognize four major subdivisions: *Psilopsida, Lycopsida, Sphenopsida,* and *Pteropsida.* In the light of continuous changes in viewpoint and nomenclature regarding the major taxa of vascular plants, the classification followed in this book may be criticized as too conservative or as outmoded. We believe, however, that there is considerable pedagogic value in this taxonomic scheme and that teachers who maintain a different viewpoint can readily adapt our presentation of comparative morphology to their own philosophy regarding the number of divisions or phyla within the vascular plants.

In each of the chapters dealing with the subdivisions or orders of vascular plants we have striven for a full and balanced treatment of the subject. Particularly with reference to those chapters on the Psilopsida, Lycopsida, and Sphenopsida, considerable paleobotanical information has been included in order to provide a historical background for the more extended discussions of the surviving types in these groups. In all chapters in this book citations to standard works and to published articles pertinent to a given topic are made directly in the text, and the complete references are listed alphabetically at the end of each chapter. Of course there is no pretense that these collectively represent a definitive bibliography. But it is believed that the references given will indicate the source of most of the interpretations adopted and will at the same time provide the student and teacher with the necessary clues to the voluminous literature relating to the morphology of vascular plants.

Illustrations are an essential component of a textbook in plant morphology, and the numerous drawings, diagrams, and photographs in this book have been carefully selected to aid the student to grasp the salient points developed in each chapter. Some of the figures are based upon original drawings and photomicrographs prepared by the authors. The great majority of the line drawings, however, have been redrawn from published articles and books by the skillful pen of Mr. Evan L. Gillespie, to whom we express our deep appreciation for enthusiastic, imaginative, and intelligent cooperation. The sources of all borrowed illustrations are indicated in the figure legends, and we are indebted to the various authors and publishers for permission to reproduce them. Special acknowledgment is made to Dr. Katherine Esau for permission to use a number of the illustrations in her book, *Plant Anatomy* (John Wiley and Sons, Inc., N. Y.). We also thank Mr. Victor Duran, who made several of the original photomicrographs, and Dr. T. E. Weier, who kindly provided a number of the photographs used in the chapter on the Coniferales.

Although the authors assume full responsibility for the viewpoints and statements in this book, special acknowledgments are due to those individuals who have offered advice and suggestions in the preparation of the manuscript. In particular we are greatly obliged to Professor Ralph H. Wetmore of Harvard University, who critically reviewed the entire manuscript and offered many valuable suggestions for its improvement. Mr. Howard J. Arnott, who served as the senior author's teaching assistant in plant morphology, and Dr. Marion S. Cave read portions of the original manuscript and were extremely helpful in discussing certain aspects of our presentation. Two of the editors of the Biology Series, Dr. George W. Beadle and Dr. Ralph Emerson, reviewed the manuscript, and we are grateful for their help and valuable suggestions. Lastly, we are happy to pay deserved tribute to our wives, Helen V. Foster and Jean D. Gifford, for their unfailing patience and for their assistance with the proofreading.

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ADRIANCE S. FOSTER
ERNEST M. GIFFORD, JR.

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1 THE SCIENCE OF PLANT MORPHOLOGY

The extraordinary diversity in the form, stature, and habit of plants is a familiar fact of experience which is recognized by even the scientifically untrained observer. The "sea-weeds" of the ocean, the lowly "mosses" and graceful "ferns" of the woodlands, the towering cone-bearing trees of the northern forests, and the infinitely varied flowering plants of orchard and garden all are recognized as different kinds of plants by the layman, on the basis of more or less superficial criteria or earmarks.

Casual inspection of the *surface aspects* of plants, however, is a highly unreliable method for either separating plants into natural groups or gaining a proper understanding of the nature and relationships of their parts. Thus, for example, the small green plants floating on the surface of ponds or garden pools are often commonly lumped together as "pond scum," "algae" or even "moss," because of their small size and the absence of conspicuous flowers. However, rigorous scientific study of such a population of aquatic plants from the standpoint of morphology would show that it contains not only algae (in the scientific sense) but also aquatic ferns and minute flowering plants! With respect to the recognition of external similarities and differences among land plants, superficial observation often leads to equally incorrect conclusions. Frequently a wide variety of totally unrelated plants are called ferns by the layman, because they have divided or pinnatifid leaves. From a broad, comparative-morphological standpoint it is clear that the true ferns are remarkably diversified as to leaf form and that their distinguishing characteristics are based on subtle but reliable similarities of structure and method of reproduction. And last there is confusion in the mind of the untrained observer in regard to flowering plants. With an understandable mental picture of a conspicuous and brightly-colored garden or hothouse type of flower, the layman often fails to realize that the reproductive structures of grasses and of many trees and shrubs are flowers. This commonly leads to a wholly erroneous notion of the nature of reproduction in even the most common plants and to an astonishing underestimation of the diversity in form and habit of the flowering plants as a whole.

In marked contrast with such undisciplined regard of form and structure, the science of plant morphology attempts, by rigorous techniques and meticulous observations, to probe beneath these surface aspects of plants—in short, to explore and to compare those *hidden aspects* of form, structure, and reproduction which constitute the basis for the interpretation of similarities and differences among plants. One of the most fruitful results of early morphological studies was the recognition that a relatively few fundamental types of organs underly the construction of the plant body. Thus, the leaf, stem, and root were regarded as the principal types of vegetative organs, the size, form, proportions, and arrangement of which are subject to the most varied development or modification. As knowledge of the reproductive cycles of plants increased, sporangia and gametangia were added to this short list of major organ categories, and the importance of a broad comparative study of the resemblances, or homologies, of plant organs thus became established. Let us examine more closely the notion of homology as it is used in the interpretation of plant form and structure.

The Concept of Homology

The essence of the idea of homology was expressed in the writings of the great poet and philosopher Goethe, to whom we also owe the word "morphology" (literally the science of form). Goethe sought for the nature of the morphological relationships among the various kinds of leafy appendages in higher plants. In his celebrated essay, *Metamorphosis in Plants,* published in 1790, he concluded that no real boundary exists between such organs as cotyledons, foliage leaves, bracts, and the organs of the flower—all are expressions of the same type of organ; i.e., the leaf (Arber, 1946). Although Goethe's theory has been criticized as an example of idealistic morphology, it has proved an extremely astute viewpoint and indeed constitutes the theoretical basis for the current view that the flower is a determinate axis with foliar appendages (see, Chapter 18).

The rapid expansion of botanical knowledge which occurred in the nineteenth century emphasized the importance of the concept of homology and the need for interpreting homologies in the broadest possible light. Goethe's ideas, and the earlier observations of K. F. Wolff (1759) on the origin of leaves at the growing point of the shoot, paved the way to a better understanding of serial homology in plants. With reference to a shoot, this term designates the equivalence in *method of origin* and *positional relationships* of the successive foliar appendages of a shoot. Thus, a bud scale is considered serially homologous with a foliage leaf because, like the latter, it arises as a lateral outgrowth from the shoot apex. Classical as well as modern ontogenetic studies have shown the very close resemblances in detail of origin and early histogenesis among the varied types of foliar organs of both vegetative and flowering shoots. Moreover, the different types of foliar appendages in the same plant are often interconnected by intermediate forms or transitional organs. On the other hand, the concept of general homology in plants is much more difficult to demonstrate ontogenetically (see Mason, 1957, for a critical discussion). This is so because, unlike higher animals, plants are characterized by an open type of growth—a plant embryo is not a miniature of the adult, and hence homologies based on the resemblance in position, development, and form of two organs in different kinds of plants may be open to serious question. The cotyledons of seed plants occur at the first node of the embryo and in that respect may be held to be homologous with one another. But whether, for example, *all* foliage leaves in vascular plants at large are homologous is a question which is by no means easily resolved, either from an ontogenetic or phylogenetic point of view (see Chapter 3).

The question of homologies in plants was placed in an entirely new position as the result of the publication in 1859 of Charles Darwin's classic, *The Origin of Species*. His theory of the rôle of natural selection in producing the gradual adaptive changes in the form and organography of both plants and animals exerted a profound effect on all questions of homologies. The goal of morphology now became very clear: the interpretation of form and structure from a historical (i.e., phylogenetic) point of view. Resemblances or homologies between organs were to be viewed as the result of descent from a common ancestral "type." Thus, the strong trend toward the phylogenetic interpretation of form and structure which arose during the latter part of the past century has continued to this day. In addition to its effect on all concepts of homology, the phylogenetic approach to morphology has provided the basis for a more realistic and natural classification of the plant kingdom.

It is evident that reliable interpretations require consideration of evidence that is derived from a wide variety of sources. Morphological theories increase in probability in relation to the extent to which collateral lines of evidence can be harmonized with one another. This chapter may therefore be most appropriately concluded by a brief, critical review of the sources of evidence which should be considered and evaluated in interpreting any problems of form and structure in plants.

Sources of Evidence in Morphological Interpretation

Adult Form and Structure

By far, the most voluminous data of comparative morphology have resulted from the study of the form of the adult plant.* Information derived from such study has contributed significantly to our knowledge of the wide variations in: (1) the form, venation, and phyllotaxy (arrangement on the axis) of foliar organs, (2) the patterns of branching of root and shoot systems, and (3) the morphological construction of such spore-producing structures as sporophylls, strobili, and flowers. During the second half of the nineteenth century, increasing emphasis was placed upon the study of the primary vascular system of the plant as the key to the interpretation of the morphological nature or homology of plant organs. The wide and continued use today of vascular patterns in morphology is based upon the fundamental assumption that the

* Strictly speaking, the term "adult" cannot have the same meaning for individual higher plants as it does for individual animals; e.g., vertebrates. In vertebrates the process of embryogeny yields a truly adult organism in which normally no additional organs are produced during the lifetime of the individual. But in vascular plants the continued activity of embryonic regions or meristems at the tips of shoots and roots results in an open system of growth that is characterized by the formation of new organs throughout the life span of the individual (Fig. 1-1). Moreover, in many vascular plants the vascular cambium makes more or less extensive periodic additions to the secondary vascular system of the older portions of stems and roots. For convenience in exposition therefore, adult will designate fully developed organs or plant tissues rather than the plant as a whole.

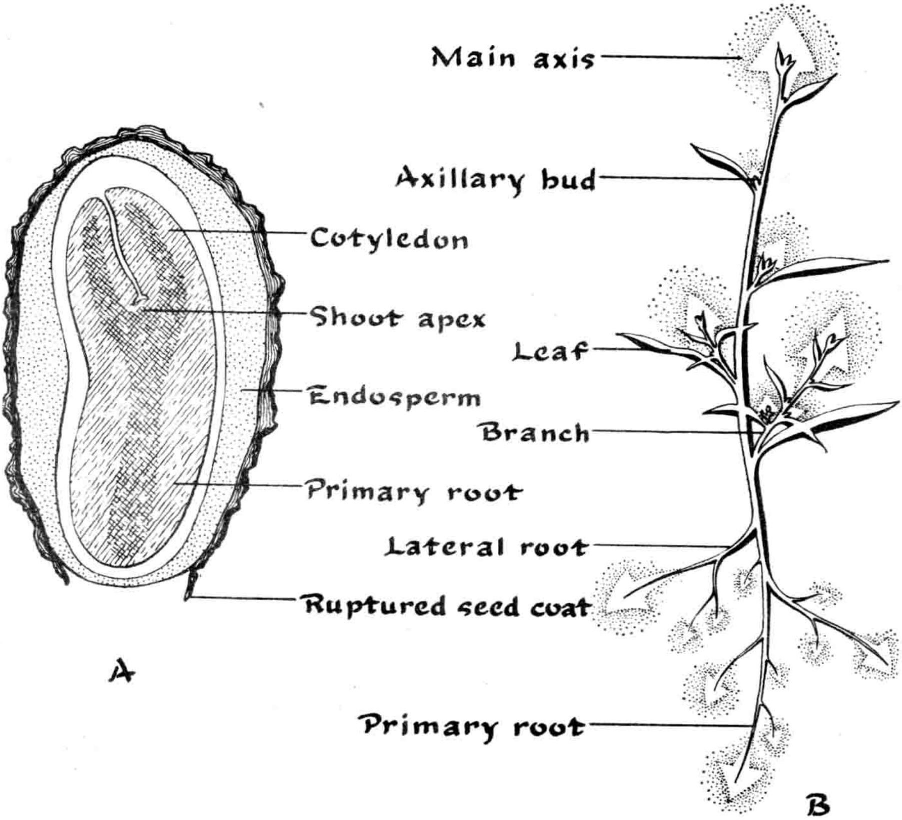

Figure 1-1 Open system of growth in vascular plants. **A,** longisection of seed of a dicotyledon showing simple organography of embryo; **B,** diagram showing the open pattern of terminal growth and the progressive formation of organs in the shoot and root systems of a young sporophyte. [A, redrawn from Avery, *Amer. Jour. Bot.* 20:309, 1933.]

primary vascular system is more stable, or conservative, in a phylogenetic sense, than other tissue systems and hence is reliable as a criterion in morphological interpretation. Considerable support for this assumption is provided not only from comparative study of living plants but also by the beautifully preserved patterns of vasculation in the vegetative and reproductive structures of extinct plants. Among the many examples which might be given of the use of vascular anatomy in the determination of homologies, the following are outstanding: the morphological interpretation of floral organs (see Chapter 18 for details); the interpretation of the phylogenetic development of the leaf traces in vascular plants (that is, the significance of the number of vascular stands which diverge into a leaf at a node); and the patterns of development of the primary xylem in the stem and root in primitive as compared with advanced plants. In addition to the emphasis on primary vascular systems, much attention has also been given to extensive surveys of the minute structure or histology of *secondary xylem*, or wood. The results of such surveys have been applied in the appraisal of the taxonomic aspects of genera and families in the seed plants, and particularly in the effort to determine the origin and trends of evolutionary specialization of tracheids and vessels (Metcalfe and Chalk, 1950; Bailey, 1954).

The Fossil Record

A salient problem common to all phylogenetic interpretations is the difficulty of determining the sequence in the evolutionary development of organs, tissues, and cells. A complete fossil record of the evolutionary history of the sporangium or the leaf would provide evidence of the origin and trends of specialization of these important structures in vascular plants; unfortunately, however, the known fossil record, as revealed by paleobotanical studies, is extremely fragmentary. Consequently, phylogenetic theories are still based largely on circumstantial or indirect evidence derived from the comparative study of living plants. The history of plant morphology is replete with examples of how the same series of morphological types has been interpreted by some investigators as a sequence of *advancing complexity*, and by others as a series in *progressive reduction*. In other words, the decision whether a given structure is primitive or advanced depends upon the interpretation of the apparently "simple" forms in the series; that is, these forms may be regarded as either the beginnings or as terminal specializations. Many simple forms which were regarded in the past as primitive now seem to be specialized because of profound evolutionary reduction. Therefore it is clear that inferences regarding the phylogenetic nature of an organ must be based upon the wise evaluation of the evidence from extinct as well as living types of plants. New paleobotanical discoveries will continue to force morphologists to reconsider and revise many of the so-called classical viewpoints that are based solely on living plants.

Aside from impressions or casts of leaves, stems, and other structures, the most important type of fossil material consists of the partially or fully preserved remains of the organs and tissues of vascular plants. The epidermis (including its distinctive stomata) is often beautifully preserved and has been utilized by Florin (1931) in his highly significant studies on the evolutionary history of gymnosperms. Much has also been learned about the structure of the conducting systems in the earliest land plants, and this information furnishes a realistic background for theoretical interpretations of patterns of vasculation in living plants (Bower, 1935). Reproductive structures such as sporangia, spores, cones, fruits, and seeds are also found in a remarkably good state of preservation, and their careful study by paleobotanists and morphologists has contributed significantly to our reconstruction of plant life in the ancient world and to continued revisions of the relationship and classification of plants (Arnold, 1947).

In concluding this brief discussion, it must be emphasized that the facts revealed by the fossil record have demonstrated the probability of parallel evolution or homoplasy in plants. These terms indicate independent origin and evolutionary development, in widely separated groups, of apparently similar structures. An excellent example of parallel evolution is the independent development of seeds in a number of clearly distinct groups of plants. Some of these groups, such as the Bennettitales, represent extinct gymnosperms and there is little evidence that this order constituted the ancestral stock from which other groups of modern seed-bearing plants arose. If one accepts the idea of parallel evolution—and many facts could be cited in its support—it is clear that great caution must be observed in postulating a monophyletic origin (i.e., from the same ancestral stock) of such fundamental morphological structures as leaves, seeds, or sporangia. All of these structures may have originated in more than one way in the evolution of various groups of living and extinct plants.

Ontogeny

A highly important source of evidence for morphological interpretation is derived from the study of ontogeny—the actual development of a plant or of one of its component organs, tissues, or cells from the primordial stage to maturity. Histogenesis is a phase of ontogenetic study concerned with the origin of cells and tissues, and embryogenesis and organogenesis are concerned with the history of development of