ARNOLD — AN INTRODUCTION TO PALEOBOTANY

# AN INTRODUCTION TO
# PALEOBOTANY

*By CHESTER A. ARNOLD*

*Professor of Botany*
*and Curator of Fossil Plants*
*University of Michigan*

FIRST EDITION
SECOND IMPRESSION

NEW YORK AND LONDON
McGRAW-HILL BOOK COMPANY, INC.
1947

# PREFACE

The preparation of this book was motivated by a longfelt need for a concise yet fairly comprehensive textbook of paleobotany for use in American colleges and universities. Although separate courses in paleobotany are not offered in many institutions, fossil plants are frequently treated in regular courses in botany and paleontology. In these courses both student and instructor are often compelled to resort to widely scattered publications, which are not always conveniently available. Lack of ready access to sources of information has retarded instruction in paleobotany and has lessened the number of students specializing in this field. Another effect no less serious has been the frequent lack of appreciation by botanists and paleontologists of the importance of fossil plants in biological and geological science.

The two works of reference principally used by British and American students of paleobotany within recent decades have been Seward's "Fossil Plants" and Scott's "Studies in Fossil Botany," the former consisting of four volumes published at intervals between 1898 and 1917, and the latter of two volumes, the last edition of which appeared in 1920 and 1923. Both are now out of print, and although they will continue to occupy a prominent place among the great works in paleobotany, they are already in many respects obsolete. Since the publication of the last edition of Scott's "Studies," many new and important discoveries have been made, which have not only added greatly to our knowledge of fossil plants but which have altered our interpretations of some of them. Many of the newer contributions have resulted from techniques scarcely known to the writers of the first quarter of the present century. These new techniques have also brought about certain shifts of emphasis, which are evident when one compares certain portions of this book with the writings of 30 years ago.

The arrangement and scope of the subject matter is in part the result of 17 years of experience in teaching a small course in paleobotany open to advanced undergraduate and graduate students, most of whom were majors or minors in botany or biology. The approach to the subject is therefore essentially botanical. Paleobotany as a subdivision of paleontology can be treated either biologically or geologically, but the two approaches are so different that to try to combine them would result only in confusion and lack of clarity. The present arrangement, therefore, is followed partly because of the necessity of making a choice, but mostly because of the author's conviction that it is best for instructional purposes. The author is not unaware of the preoccupation with paleobotany of many geologists who might with good reason prefer a presentation following the geologic time scale. Their requirements are met to some extent by the inclusion of the chapter on The Sequence of the Plant World in Geologic Time, in which an effort is made to summarize the floras of the eras and periods. Then, in dealing with some of the plant groups, the most ancient members are described first, thereby giving some idea of the major steps in development from their first appearance down to the present.

In making selections of subject matter an author can hardly avoid being partial to his particular interests to the neglect of other material. In spite of an effort to avoid bias, the ready admission is made that this book is not free from it. In order to keep the volume within practical size limits, much important material had to be rejected arbitrarily. The work of Americans has been heavily drawn upon because there is a wealth of information on fossil plants of the Western Hemisphere that has been only casually, if at all, utilized by European textbook writers and that deserves to be emphasized in a book intended to meet the needs of American students. Wherever possible North American plants are used for description and illustration in place of the more familiar and more often figured Old World forms. This book, therefore, will not serve as a substitute for the larger and more comprehensive works on paleobotany, which advanced students will still find indispensable. For them its main value will be the presentation of new developments and new points of view.

Although American fossil plants have been given more emphasis than heretofore, the author has not neglected to stress discoveries which have come to be looked upon as landmarks in paleobotany. Brongniart's classification of Paleozoic fernlike foliage, Grand'Eury's elucidation of the Paleozoic gymnosperms, the discovery of the seed-ferns by Oliver and Scott, and the labors of Kidston and Lang on the plants of the Rhynie Chert all taken together constitute a major part of the framework of present-day paleobotany, and failure to place due emphasis on them would give a distorted and incomplete view of the whole subject.

Whenever possible new and original illustrations are provided, but when previously published ones are used an effort has been made to select those which have not been previously copied in textbooks. The reader may notice that many of the familiar textbook figures are absent. With only two or three exceptions all the original photographs were made by the author, as were also most of the line drawings and diagrams.

Some of the more difficult drawings were prepared by Eduardo Salgado, Philippine botanical artist employed at the University of Michigan. Most of the photographed specimens are in the collections of the Museum of Paleontology of the same institution.

Because most of the manuscript was written during the course of the Second World War, it was not possible to correspond as freely as was desired with foreign paleobotanists, and consequently the author has been forced to rely upon his own judgment concerning some matters where counsel from colleagues abroad would have been of value. Dr. Ralph W. Chaney very obligingly read and gave constructive criticisms of the chapter on flowering plants. For this the author is indeed grateful. For photographs and figures submitted by others, individual acknowledgments are made where they appear in the text.

Geological names, when applied to North America, conform in most instances to the accepted practice of the United States Geological Survey. For foreign countries the terminology current in each country is used.

CHESTER A. ARNOLD

ANN ARBOR, MICH.,
*July*, 1947

# CONTENTS

# CHAPTER I

## INTRODUCTION

Paleobotany is the study of the plant life of the geologic past. It is a part of the more comprehensive science of paleontology, although in general practice the latter is concerned mainly with animal remains, and plants receive only brief consideration. Just as paleontology is outlined by the overlap of the realms of biology and geology, paleobotany rests upon botanical and geological foundations. So inseparable is it from these basic sciences that except for taxonomic terms it has no terminology exclusively its own, but it utilizes those technical appellations that have become standardized for living plants and for the rock formations in which the plants are preserved.

Paleobotany can be approached from the viewpoint of botany, wherein emphasis is placed upon the plant, or from the geological angle in which the rock containing the fossils is the primary concern. Whatever the purpose in studying fossil plants may be, an intimate and thorough knowledge of the principles of both botany and geology is essential for a complete understanding of the subject.

Our knowledge of the plant life of the past has been assembled from the fragmentary fossil remains preserved in stratified rocks. These rocks are superimposed upon one another in series, with the older ones at the bottom and the younger ones toward the top. The layers vary greatly in thickness, composition, and lateral extent. Some lie nearly horizontal and maintain a fairly uniform thickness over large areas. Others may be thick at one place and thin at other places, or they may be localized and disappear altogether when traced for short distances. These differences in vertical and lateral extent are dependent upon the circumstances under which the rocks were formed and upon the amount of erosion to which they have been subjected since their formation. Stratified rocks are built up of sediments that accumulate in the bottoms of seas, lakes, lagoons, swamps, subsiding beaches, and flooded valleys.

The sequence of the stratified rocks is rendered visible to us chiefly through the processes of erosion. Streams everywhere cut deeply into the underlying formations and expose them to view in the walls of ravines and canyons (Figs. 1 and 3) and on the more gently sloping sides of valleys. Waves carve high and often fantastic cliffs along the coast

(Fig. 2), and differential erosion frequently produces striking landscape features on the surface of the land. In addition to the work of natural forces, the activities of man have uncovered the strata in otherwise unexposed places by means of drill holes, mine shafts, quarries, and railroad and highway excavations.

The total thickness of sediments that have accumulated since the beginning of decipherable geologic time amounts to several miles, but at no place on the surface of the earth is the entire sequence visible. This

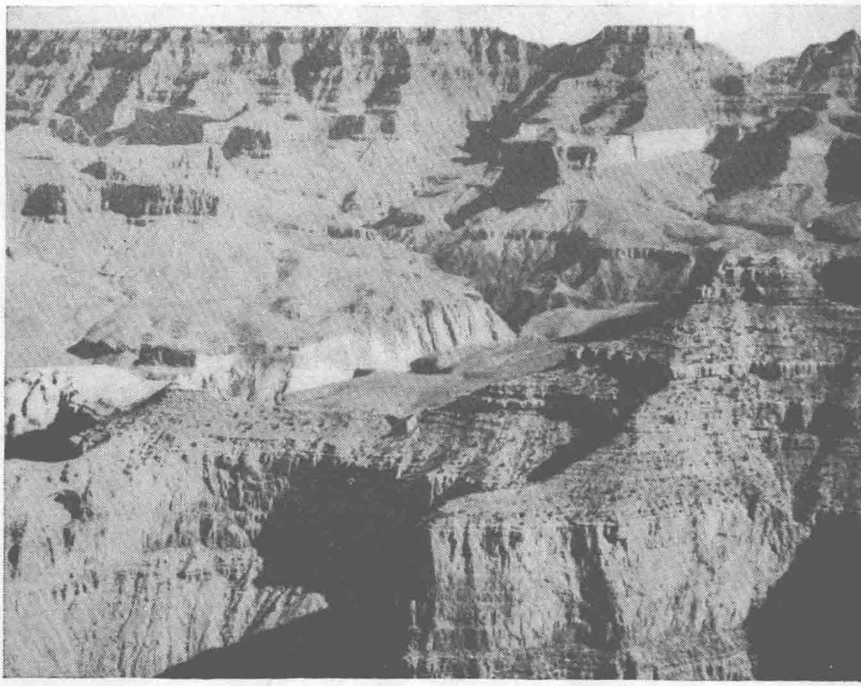

FIG. 1.—View of part of the Grand Canyon of the Colorado River. The formations exposed to view range from the pre-Cambrian to the Permian. This is probably the most striking manifestation of stream erosion of sedimentary strata anywhere in the world.

is because nowhere, with the possible exception of some places in the deepest parts of the ocean, has deposition been going on continuously at any one place without interruption from the beginning. Subsidence of the land below water level, which is ordinarily necessary for the deposition of sediments, is followed after time intervals of varying lengths by elevation above the water, and then erosion may again remove part or all of the deposit. The material thus eroded is redeposited in adjacent areas. The deposition and formation of stratified rocks therefore go on intermittently within any particular area. The stratigraphic sequence therefore within any particular region will often show interruptions. These interruptions, which are caused by cycles of deposition and erosion, are called "unconformities." An unconformity may represent a time lapse of almost any length. Unconformities may be recognized by the difference in the character of the rocks above and below the break, or by means of conspicuous differences in the fossil content. Then there are other factors that may disturb the orderly sequence of rock strata. Some of these are faulting, folding, solution, and intrusions of lava.

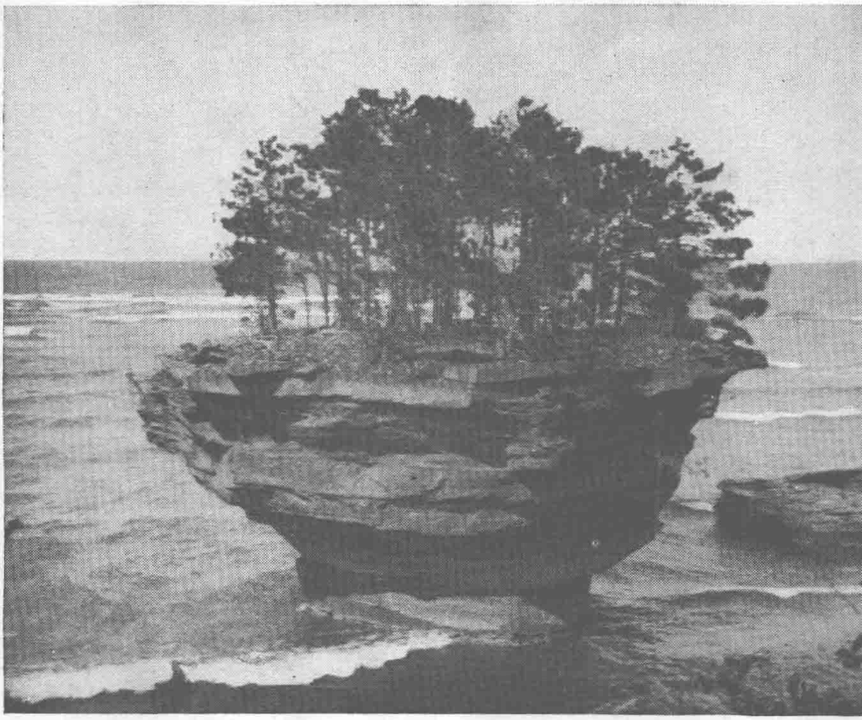

FIG. 2.—Turnip Rock, along the shore of Lake Huron, Huron County Michigan. This rock is the result of the under-cutting of Mississippian sandstone by wave action.

The primeval rocks of the surface of the earth were igneous and crystalline, but before the beginning of decipherable time the processes of erosion had been at work for millions of years removing particles of rock from the higher places and depositing them in depressions and hollows. Thus by the time the oldest known life had come into existence, the original surface of the land had been rebuilt to a considerable extent. It is probable that at no place on the earth are the first formed rocks preserved at the surface. Even extremely ancient ones such as those which constitute the Adirondack Mountains or the Canadian Shield show evidence of transportation and deposition of the component materials similar to that which was responsible for the formation of the rocks of later ages.

The major divisions of geologic time (the eras) are based principally upon the life that characterized them as revealed by the fossil content of the rocks. The oldest rocks that can be satisfactorily dated belong to the long era known as the "pre-Cambrian." Evidences of life during this time consist mainly of limestones thought to be of algal origin, problematic bacteria, and marks probably representing the trails of primitive

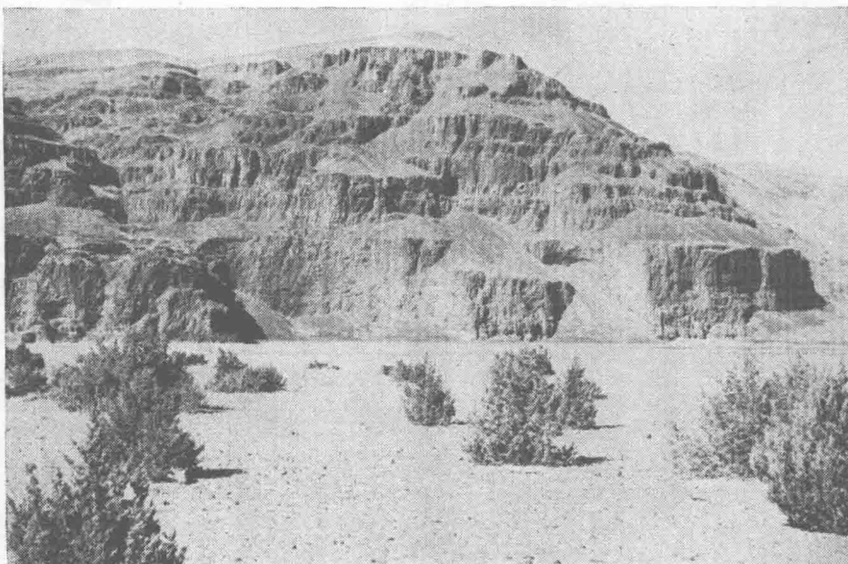

FIG. 3.—Tertiary basalt formation along the Columbia River near Vantage Bridge, Washington. The superimposed layers are the result of a succession of lava flows. Lava sheets like these are frequently interbedded with layers of ash which furnish an excellent environment for the preservation of leaf compressions and petrified parts.

wormlike organisms. Then came the Paleozoic era, with a multitude of marine invertebrates, fishes and amphibians, and spore-bearing plants such as lycopods, scouring rushes and ferns, and naked-seeded plants belonging to the Pteridospermae and the Cordaitales. It was during the early or middle Paleozoic that land vegetation appeared upon the earth. The Mesozoic was the age of dinosaurs, and its seas were populated with giant squids and ammonites. It was also an age of gymnosperms, as evidenced by the abundance of cycadophytes and conifers. Toward the end of the Mesozoic the flowering plants underwent a phenomenal development to become the dominant plant group that they are today. The rapid rise of the flowering plants near the end of the Mesozoic was

Geologic Time Table as Adopted by the United States Geological Survey

| Era | Period (System) | Epoch (Series) |
|---|---|---|
| Cenozoic | Quaternary | Recent |
| | | Pleistocene |
| | Tertiary | Pliocene |
| | | Miocene |
| | | Oligocene |
| | | Eocene |
| Mesozoic | Cretaceous | Upper |
| | | Lower |
| | Jurassic | Upper |
| | | Middle |
| | | Lower |
| | Triassic | Upper |
| | | Middle |
| | | Lower |
| Paleozoic | Carboniferous | Permian |
| | | Pennsylvanian |
| | | Mississippian |
| | Devonian | Upper |
| | | Middle |
| | | Lower |
| | Silurian | |
| | Ordovician | Upper |
| | | Middle |
| | | Lower |
| | Cambrian | Saratogan |
| | | Acadian |
| | | Waucoban |
| Proterozoic—pre-Cambrian | | |

followed by the spread of land mammals, which marked the beginning of the Cenozoic.

The geological approach to the subject of paleobotany is mainly from the standpoint of the correlation of rock formations. Fossils are the markers of geologic time. For purposes of correlation, plant fossils are used either alone or as supplements to animal fossils. Rocks in widely separated localities containing similar floras and faunas are usually assumed to be of approximately the same age. The largest divisions of geologic time (the eras) are based upon the presence in the rocks of major groups of organisms, and the smaller units are demarked in turn by lesser groups. Final subdivisions may rest upon the presence of certain genera or species, or sometimes merely upon the relative abundance of a species or a group of species. Sometimes, however, there are discrepancies in the age as indicated by the fauna and by the flora. If we assume that the organisms are correctly determined, such discrepancies may be due to unexplained environmental factors under which the organisms lived. Those animals most used for correlation are marine invertebrates, which represent an aquatic environment. Plants, with the exception of algae, are mostly terrestrial. The greatest age discrepancies occur in rocks representing periods during which rapid faunal and floral changes were taking place. Sometimes both sets of organisms did not change at the same rate, with the result that an older fauna may overlap a younger flora, or vice versa. Usually, however, major floral changes have occurred first during geological time, to be followed by changes of similar magnitude in the fauna. For example, the Mesozoic flora began to develop in the Permian, and the plant groups that characterize the Cenozoic had become well established in the Upper Cretaceous. Thus in at least two instances during the geologic past, large-scale plant evolution has preceded comparable progress in animal evolution by a time interval approximately equal to one-half of a period.

From the botanical standpoint the aims and the objectives of paleobotany are not essentially different from those of the study of living plants insofar as they pertain to the interpretation of structure, morphology, distribution, phylogeny, and ecology. Paleobotany differs from other branches of botany principally in the techniques employed. Petrifactions require special equipment for sectioning, and various chemical treatments are often used for removing opaque substances or for swelling the tissues in compressions and in lignitized and bituminized remains. Incomplete preservation is usually the limiting factor in the study of fossil plants because the plants are seldom found whole with all parts present and all tissues intact. As a result of the fragmentary condition of most fossil plants, the bulk of the paleobotanical knowledge extant today has been assembled piece by piece from numerous detached and often isolated parts.

The task of classifying fossil plants is not only difficult, but is fraught with numerous chances for error. The paleobotanist must frequently work with plants belonging not only to extinct genera and species, but to extinct families or orders or even classes of the plant kingdom. In general it may be said (although many exceptions must be allowed) that the older a fossil plant is, the wider the categorical rank becomes which will include both it and its nearest living equivalents. For example, most of the Miocene conifers found in North America can be identified as the same as or very close to species that are in existence somewhere on the earth at the present time, but in the late Mesozoic it is usually possible to identify them only to genera. They seem to belong for the most part to extinct species. Then in the Jurassic modern coniferous genera are difficult to recognize with certainty, but the remains can sometimes be assigned to families that have modern representatives. In the late Paleozoic, where the conifers first appear in the fossil record, they cannot be classified with the living conifers into groups smaller than orders. Before this, all known gymnosperms belong to extinct orders and probably to extinct classes. Therefore, since the paleobotanist is often confronted with plants belonging to extinct groups, the foliage, stems, and reproductive organs may appear strange and unlike those exhibited by any living plants with which he is familiar. For a proper understanding of these ancient plants, the investigator must be equipped with a thorough knowledge of a wide range of plant forms and should be well versed in the essential characteristics of the families, orders, classes, and divisions of recent plants. This knowledge may then serve as a basis for the classification of the ancient forms. Classification and naming, however, are not the only objectives in the study of fossils. One also endeavors to learn as much as possible about the plants as organisms —how they grew, how they reproduced, and what their environmental adaptations might have been.

The facts derived from a study of fossil plants are of paramount importance for the bearing they have had on the broader subjects of phylogeny and evolution. It has long been hoped that extinct plants will ultimately reveal some of the stages through which existing groups have passed during the course of their development, but it must be freely admitted that this aspiration has been fulfilled to a very slight extent, even though paleobotanical research has been in progress for more than one hundred years. As yet we have not been able to trace the phylogenetic history of a single group of modern plants from its beginning to the present. The phylogeny of plants is much less understood than that pertaining to some groups of animals, such as the horses and elephants, for example. Two factors account for this (1) the imperfections of the fossil record, and (2) disagreement as to the meaning of various characteristics in a natural system of classification. Furthermore, different parts of plants have not always evolved to an equal extent or at the same rate, and within unrelated series of plants comparable parts have often developed along parallel lines. Whether these phenomena are the results of unknown factors in the environment or of other forces is not clear, but the fact remains that great caution must be exercised in postulating relationships on the basis of a few structural similarities. Some of the outstanding examples of parallel development revealed by fossil plants are the production of seedlike bodies by certain of the Paleozoic lycopods and the development of elaborate floral organs resembling the flowers of angiosperms in the Mesozoic cycadeoids. These examples do not mean that the lycopods are intimately related to any of the gymnosperms or flowering plants or that the cycadeoids were in line with flowering plant evolution. The independent formation of secondary wood in various plant groups is another outstanding example of parallel development. At some time during the past this tissue has appeared in some members at least of practically all the vascular plant groups. Resemblances that are the result of parallel development also extend to habit. The superficial resemblance of the stem and foliage of *Casuarina*, an angiosperm, to *Equisetum* is well known. Conversely, closely related plants may develop along noticeably different lines. The Paleozoic lepidodendrids and sigillarians are examples of lycopods which became large trees quite different from the small and inconspicuous species which make up the lycopod group at the present time.

The main contribution of paleobotany to natural science has been a more adequate picture than could be gained from living plants alone of the relative importance of the different groups constituting the plant kingdom. For example, paleobotanical studies have shown us that one of the smallest of living plant groups, the Equisetales, has a long history, and when regarded in the light of its past, is an assemblage of a number of families. Not only were the Equisetales at one time a large group, but at the height of their development there existed contemporaneously other closely allied groups that have been extinct for millions of years. The fossil records of the genus *Ginkgo* reveal a similar history. *Ginkgo biloba* is the lone survivor of an order of gymnosperms that contained a dozen or more genera during Mesozoic times. The lycopods and ferns have similar records. In addition to showing the true status of Recent plant groups in the past, paleobotanical research has brought to light the existence during the past of others which are entirely extinct and have left no near relatives, examples being the Psilophytales and the "seed-ferns," both from the Paleozoic. The influence of a knowledge of extinct plants on our concept of relationships between living types has been profound.

During the past many plant groups arose to a place of prominence, only to decline and have their place taken by others. Plant evolution, therefore, has not always been progressive, but has involved innumerable changes and constant experimentation with new types. The fossil record is replete with examples of the development of elaborate vegetative and reproductive structures in plant groups of which the recent members are considered primitive. Examples are the seedlike organs of some of the ancient lycopods, the complex strobili of *Cheirostrobus*, and the "flowers" of the Mesozoic cycadeoids. These structures all represent extreme specialization along particular lines within restricted groups. However, this was accompanied by corresponding loss of plasticity, and when the plants were confronted with far-reaching environmental changes they were unable to modify themselves sufficiently to cope with the new conditions. In plants, as with many animals, the highest state of development was often attained just prior to complete or near extinction.

A fact that has been well emphasized by paleobotanical studies is that the increase in complexity of plants seen in the Thallophyta, Bryophyta, Pteridophyta, and Spermatophyta series, and which was once the central theme of morphological thought, does not depict a phylogenetic sequence. It is still tenable that the Thallophyta were probably the starting point for all higher plant evolution, but it is more than likely that several of the higher types have evolved from this group independently of each other. There is no reason whatsoever to suppose that the so-called Pteridophyta arose as one complex from the Bryophyta, or that seed plants evolved as one type from the pteridophytes. The terms Pteridophyta and Spermatophyta do not embrace natural, or in all cases, even closely related groups, but they include several assemblages having independent origins. For example, the fossil record shows the lycopods and scouring rushes to be independent lines as far into the past as they can be traced. The same is true with respect to either of these types and the ferns. Moreover, the seed plants can be traced to a period almost as remote as the ferns. When, and from what earlier forms seed plants originated, we can only guess, although it is quite reasonable to assume that their ancestors were spore producers of some kind, maybe ancient fernlike plants, or possibly even the more primitive members of the very ancient Psilophytales. However, it is not advisable to assume that all seed plants arose from the same source. There is no proof that the conifers and cycads had a common origin, and the problem of flowering plant origin is the most enigmatic of all.

## Classification of Plants

The reason for classifying plants is to facilitate the arrangement of the different kinds into an orderly sequence so that their relationships to one another can be better understood. The older systems were based entirely upon living plants and whatever information was available concerning fossil species was utilized little or not at all. Before 1900, however, it became apparent that fossil plants revealed many facts concerning the status of some groups that are not expressed by living plants, and since that date the influence of paleobotany upon classification has become increasingly apparent.

There is no perfect and final classification of plants. Several systems are in use at the present time, and each has its stanch advocates. Those which are in use and which seem quite satisfactory today may be obsolete tomorrow, when they will be replaced by others more in accord with advancing knowledge, and they will be subject to change as long as a single fact concerning the morphology, cytology, structure, or life history of any species remains unknown. The system followed in this book is believed to be the one that best expresses the relationships of extinct plants, as they are now understood, to the plant kingdom as a whole.

The plant kingdom can be logically and conveniently divided into two groups, or subkingdoms, which, without the necessity of using technical terms, may be termed the *nonvascular* and the *vascular* plants. The nonvascular plants, which lack highly developed food and water-conducting tissues, consist of two divisions, (1) the *Thallophyta*, which in turn is divisible into the *Algae* and the *Fungi*, and (2) the *Bryophyta*, which consists of the *Hepaticae* (liverworts) and the *Musci* (mosses). The study of fossil plants has brought little to bear upon the structure and morphology of the nonvascular plants, so this simple and conventional scheme based upon the living members is wholly acceptable from the paleobotanical standpoint. It is upon the vascular plants that paleobotanical discoveries have had the most important bearings.

The body of the vascular plant has a highly organized food-and water-conducting structure called the "stele." It contains the xylem and the phloem. The classification scheme that has probably been used by more botanists than any other divides the vascular plants into two divisions, the *Pteridophyta* (spore bearers), and the *Spermatophyta*, (seed plants). This was the outgrowth of an older system of *Cryptogamia* and *Phanerogamia*. The former embraced all nonvascular plants and those vascular plants which reproduce directly by spores. The Phanerogamia are equivalent to the Spermatophyta.

*The Divisions.*—Under the system of Pteridophyta and Spermatophyta the main categories are as follows:

Division Pteridophyta—ferns and "fern allies"
  Class Lycopodineae—lycopods
  Class Equisetineae—scouring rushes
  Class Filicineae—ferns
Division Spermatophyta—seed plants
  Class Gymnospermae—gymnosperms
  Class Angiospermae—flowering plants

This system was founded entirely upon living forms, but with the increase in knowledge of fossil plants combined with a better understanding of the fundamental structure of the plant body, this scheme has been found to possess at least two basic weaknesses. In the first place it assumes that seed production alone is sufficient to set one group apart from another regardless of certain anatomical similarities that may exist between them. However, we know from the evidence furnished by certain fossil forms that seeds have been developed in different groups during the past, and that, when considered by itself, seed formation is not a final criterion of affinity. The second weakness is that it ignores anatomical evidences, factors which we have every reason to believe are as basic in classification as reproductive structures. From a wider knowledge of plants, both living and extinct, it now appears that a more fundamental basis for classification consists of three characters as follows: (1) nature and relation of leaf and stem, (2) vascular anatomy, and (3) position of the sporangia. On the basis of these the vascular plants may be divided into four divisions as follows:

Division Psilopsida—the Psilotales (living) and the Psilophytales (extinct). The Psilotales were usually included within the Lycopodineae in the older classification, and the Psilophytales were usually ignored because they have no living members. Sometimes they were added as a separate class, the Psilophytineae. The Psilopsida often lack leaves, and when they are present a vascular supply is absent. The sporangia are terminal on the main stem or a side branch and consist essentially of an enlargement of the stem tip containing sporogenous tissue. The assumed affinity between the Psilophytales and the Psilotales is entirely on a structural basis. They have no connection in the fossil record.

Division Lycopsida—the lycopods (Lycopodineae of the older classification). Leaves small, simple, spirally arranged and provided with a vascular system. Sporangia adaxial, sessile, and borne on or in close proximity with leaves (sporophylls). No leaf gaps are present in the primary vascular cylinder, and the exarch condition prevails.

Division Sphenopsida (also called Articulatales, Articulatineae, Arthophyta, etc.)—the scouring rushes and relatives (Equisetineae of the older classification). The stems are jointed and bear whorls of leaves at the nodes. The leaves are attached by a narrow base or are coalescent, but sometimes broadened distally. The sporangia are on specialized stalks called "sporangiophores," usually peltate or recurved.

Division Pteropsida—ferns, seed-ferns, gymnosperms, and flowering plants (Filicineae and Spermatophyta of the older classification). The members are predominantly megaphyllous and leaf gaps are present in the primary vascular cylinder of all except protostelic forms and a few of the very ancient gymnosperms. The sporangia (wherever the position is clearly determinable) are abaxial on