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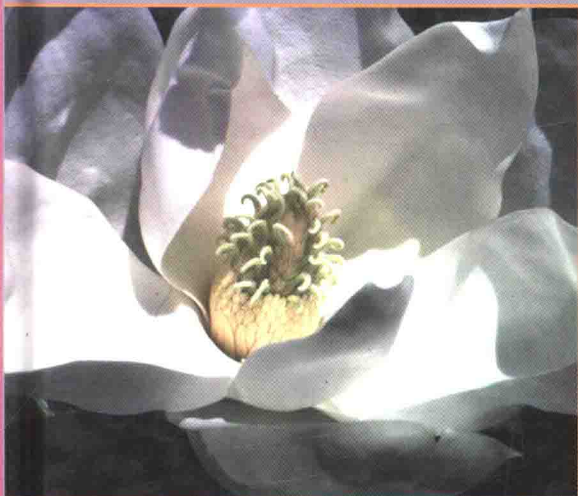
Plant Systematics








Michael G. Simpson

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PLANT SYSTEMATICS

I wish to dedicate this book to three mentors I was very fortunate to know: Albert Radford, who taught critical thinking; P. Barry Tomlinson, who taught the fine art of careful observation; and Rolf Dahlgren, whose magnetic personality was inspirational. I also wish to thank my many students who have provided useful suggestions over the years, plus three writers who captured my interest in science and the wonder of it all: Isaac Asimov, Richard Feynman, and Carl Sagan.

PREFACE

Plant Systematics is an introduction to the morphology, evolution, and classification of land plants. My objective is to present a foundation of the approach, methods, research goals, evidence, and terminology of plant systematics and to summarize information on the most recent knowledge of evolutionary relationships of plants as well as practical information vital to the field. I have tried to present the material in a condensed, clear manner, such that the beginning student can better digest the more important parts of the voluminous information in the field and acquire more detailed information from the literature.

The book is meant to serve students at the college graduate and upper undergraduate levels in plant systematics or taxonomy courses, although portions of the book may be used in flora courses and much of the book could be used in general courses in plant morphology, diversity, or general botany.

Each chapter has an expanded Table of Contents on the first page, a feature that my students recommended as very useful. Numerous line drawings and color photographs are used throughout. A key feature is that illustrated plant material is often dissected and labeled to show important diagnostic features. At the end of each chapter are (1) Review Questions, which go over the chapter material; (2) Exercises, whereby a student may apply the material; and (3) References for Further Study, listing some of the basic and recent references. Literature cited in the references is not exhaustive, so the student is encouraged to do literature searches on his/her own (see Appendix 3).

The book is classified into units, which consist of two or more chapters logically grouped together. Of course, a given instructor may choose to vary the sequence of these units or the chapters within, depending on personal preference and the availability of plant material. There is a slight amount of repetition between chapters of different units, but this was done so that chapters could be used independently of one another.

Unit 1, Systematics, gives a general overview of the concepts and methods of the field of systematics. Chapter 1 serves as an introduction to the definition, relationships, classification, and importance of plants and summarizes the basic concepts and principles of systematics, taxonomy, evolution, and phylogeny. Chapter 2 covers the details of phylogenetic systematics, and the theory and methodology for inferring phylogenetic trees or cladograms.

Unit 2, Evolution and Diversity of Plants, describes in detail the characteristics and classification of plants. The six chapters of this unit are intended to give the beginning student a basic understanding of the evolution of Green and Land Plants (Chapter 3), Vascular Plants (Chapter 4), Woody and Seed Plants (Chapter 5), and Flowering Plants (Chapters 6-8). Chapters 3-5 are formatted into two major sections. The first section presents cladograms (phylogenetic "trees"), which portray the evolutionary history of the group. Each of the major derived evolutionary features ("apomorphies") from that cladogram is described and illustrated, with emphasis on the possible adaptive significance of these features. This evolutionary approach to plant systematics makes learning the major plant groups and their features conceptually easier than simply memorizing a static list of characteristics. Treating these features as the products of unique evolutionary events brings them "to life," especially when their possible adaptive significance is pondered. The second section of Chapters 3 through 5 presents a brief survey of the diversity of the group in question. Exemplars within major groups are described and illustrated, such that the student may learn to recognize and know the basic features of the major lineages of plants.

Because they constitute the great majority of plants, the flowering plants, or angiosperms, are covered in three chapters. Chapter 6 deals with the evolution of flowering plants, describing the apomorphies for that group and presenting a brief coverage of their origin. Chapters 7 and 8 describe specific groups of flowering plants. In Chapter 7 the non-eudicot groups are treated, including basal angiosperms and the monocotyledons. Chapter 8 covers the eudicots, which make up the great majority of angiosperms. Numerous flowering plant families are described in detail, accompanied by photographs and illustrations. Reference to Chapter 9 and occasionally to Chapters 10-14 (or use of the comprehensive Glossary) may be needed with regard to the technical terms. Because of their great number, only a limited number of families are included, being those that are commonly encountered or for which material is usually available to the beginning student. I have tried to emphasize diagnostic features that a student might use to recognize a plant family, and have included some economically important uses of family members. The Angiosperm Phylogeny Group II system of classification is used throughout (with few exceptions). This system uses orders as the major taxonomic rank in grouping families of close relationship and has proven extremely useful in dealing with the tremendous diversity of the flowering plants.

Unit 3, Systematic Evidence and Descriptive Terminology, begins with a chapter on plant morphology (Chapter 9). Explanatory text, numerous diagrammatic illustrations, and photographs are used to train beginning students to precisely and thoroughly describe a plant morphologically. Appendices 1 and 2 (see below) are designed to be used along with Chapter 9. The other chapters in this unit cover the basic descriptive terminology of plant anatomy (Chapter 10), plant embryology (Chapter 11), palynology (Chapter 12), plant reproductive biology (Chapter 13), and plant molecular systematics (Chapter 14). The rationale for including these in a textbook on plant systematics is that features from these various fields are described in systematic research and are commonly utilized in phylogenetic reconstruction and taxonomic delimitation. In particular, the last chapter on plant molecular systematics reviews the basic techniques and the types of data acquired in what has perhaps become in recent years the most fruitful of endeavors in phylogenetic reconstruction.

Unit 4, Resources in Plant Systematics, discusses some basics that are essential in everyday systematic research. Plant identification (Chapter 15) contains a summary of both standard dichotomous keys and computerized polythetic keys and reviews practical identification methods. The chapter on nomenclature (Chapter 16) summarizes the basic rules of the most recent International Code of Botanical Nomenclature, including the steps needed in the valid publication of a new species and a review of botanical names. A chapter on plant collecting and documentation (Chapter 17) emphasizes both correct techniques for collecting plants and thorough data acquisition, the latter of which has become increasingly important today in biodiversity studies and conservation biology. Finally, the chapter on herbaria and data information systems (Chapter 18) reviews the basics of herbarium management, emphasizig the role of computerized database systems in plant collections for analyzing and synthesizing morphological, ecological, and biogeographic data.

Lastly, three **Appendices** and a **Glossary** are included. I have personally found each of these addenda to be of value in my own plant systematics courses. Appendix 1 is a list of characters used for detailed plant descriptions. This list is useful in training students to write descriptions suitable for publication. Appendix 2 is a brief discussion of botanical illustration. I feel that students need to learn to draw, in order to develop their observational skills. Appendix 3 is a listing of scientific journals in plant systematics, with literature exercises. The Glossary defines all terms used in the book and indicates synonyms, adjectival forms, plurals, abbreviations, and terms to compare.

By the time of publication, two Web sites will be available to be used in conjunction with the textbook: (1) a Student Resources site (http://books.elsevier.com/companion/0126444609), with material that is universally available; and (2) an Instructor Resources site (http://books.elsevier.com/manualsprotected/0126444609), with material that is password protected. Please contact your sales representative at <textbooks@elsevier.com> for access to the Instructor Resources site.

Throughout the book, I have attempted to adhere to **W-H-Y**, **W**hat-**H**ow-**W**h**y**, in organizing and clarifying chapter topics: (1) What is it? What is the topic, the basic definition? (I am repeatedly amazed that many "scientific" arguments could have been resolved at the start by a clear statement or definition of terms.) (2) How is it done? What are the materials and methods, the techniques of data acquisition, the types of data analysis? (3) Why is it done? What is the purpose, objective, or goal; What is the overriding paradigm involved? How does the current study or topic relate to others? This simple W-H-Y method, first presented to me by one of my mentors, A. E. Radford, is useful to follow in any intellectual endeavor. It is a good lesson to teach one's students, and helps both in developing good writing skills and in critically evaluating any topic.

Finally, I would like to propose that each of us, instructors and students, pause occasionally to evaluate why it is that we do what we do. Over the years I have refined my ideas and offer these suggestions as possible goals: 1) to realize and explore the beauty, grandeur, and intricacy of nature; 2) to engage in the excitement of scientific discovery; 3) to experience and share the joy of learning. It is in this spirit that I sincerely hope the book may be of use to others.

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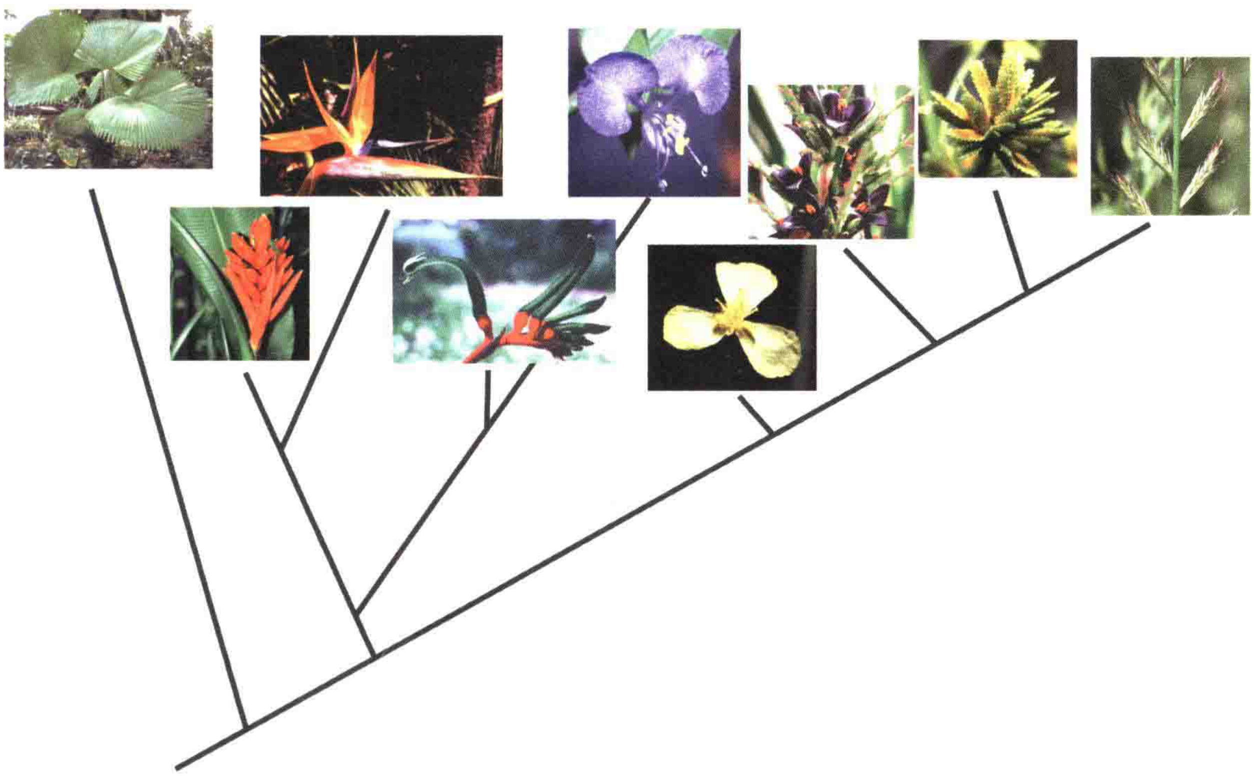
SYSTEMATICS



1

PLANT SYSTEMATICS: AN OVERVIEW

This book is about a fascinating field of biology called plant systematics. The purpose of this chapter is to introduce the basics: what a plant is, what systematics is, and the reasons for studying plant systematics.

PLANTS

WHAT IS A PLANT?

This question can be answered in either of two conceptual ways. One way, the traditional way, is to define groups of organisms such as plants by the characteristics they possess. Thus, historically, "plants" included those organisms that possess photosynthesis, cell walls, spores, and a more or less sedentary behavior. This traditional grouping of plants contained a variety of microscopic organisms, all of the "algae," and the more familiar plants that live on land. A second way to answer the question "What is a plant?" is to evaluate the evolutionary history of life and to use that history to delimit the groups of life. We now know from repeated research studies that some of the photosynthetic organisms evolved independently of one another and are not closely related.

Thus, the meaning or definition of the word *plant* can be ambiguous and can vary from person to person. Some still like to treat "plants" as an unnatural assemblage, defined by the common (but independently evolved) characteristic of photosynthesis. However, delimiting organismal groups based on evolutionary history has gained almost universal acceptance. This latter type of classification directly reflects the patterns of that evolutionary history and can be used to explicitly test evolutionary hypotheses (discussed later; see Chapter 2).

An understanding of what plants are requires an explanation of the evolution of life in general.

PLANTS AND THE EVOLUTION OF LIFE

Life is currently classified as three major groups (sometimes called domains) of organisms: **Archaea** (also called **Archaebacteria**), **Bacteria** (also called **Eubacteria**), and **Eukarya** or **eukaryotes** (also spelled eucaryotes). The evolutionary relationships of these groups are summarized in the simplified "evolutionary tree" or "cladogram" of Figure 1.1. The Archaea and Bacteria are small, mostly unicellular organisms that possess circular DNA, replicate by fission, and lack membrane-bound organelles. The two groups differ from one another in the chemical structure of certain cellular components. Eukaryotes are unicellular or multicellular organisms that possess linear DNA (organized as histone-bound chromosomes), replicate by mitotic and often meiotic division, and possess membrane-bound organelles such as nuclei, cytoskeletal structures, and (in almost all) mitochondria (Figure 1.1).

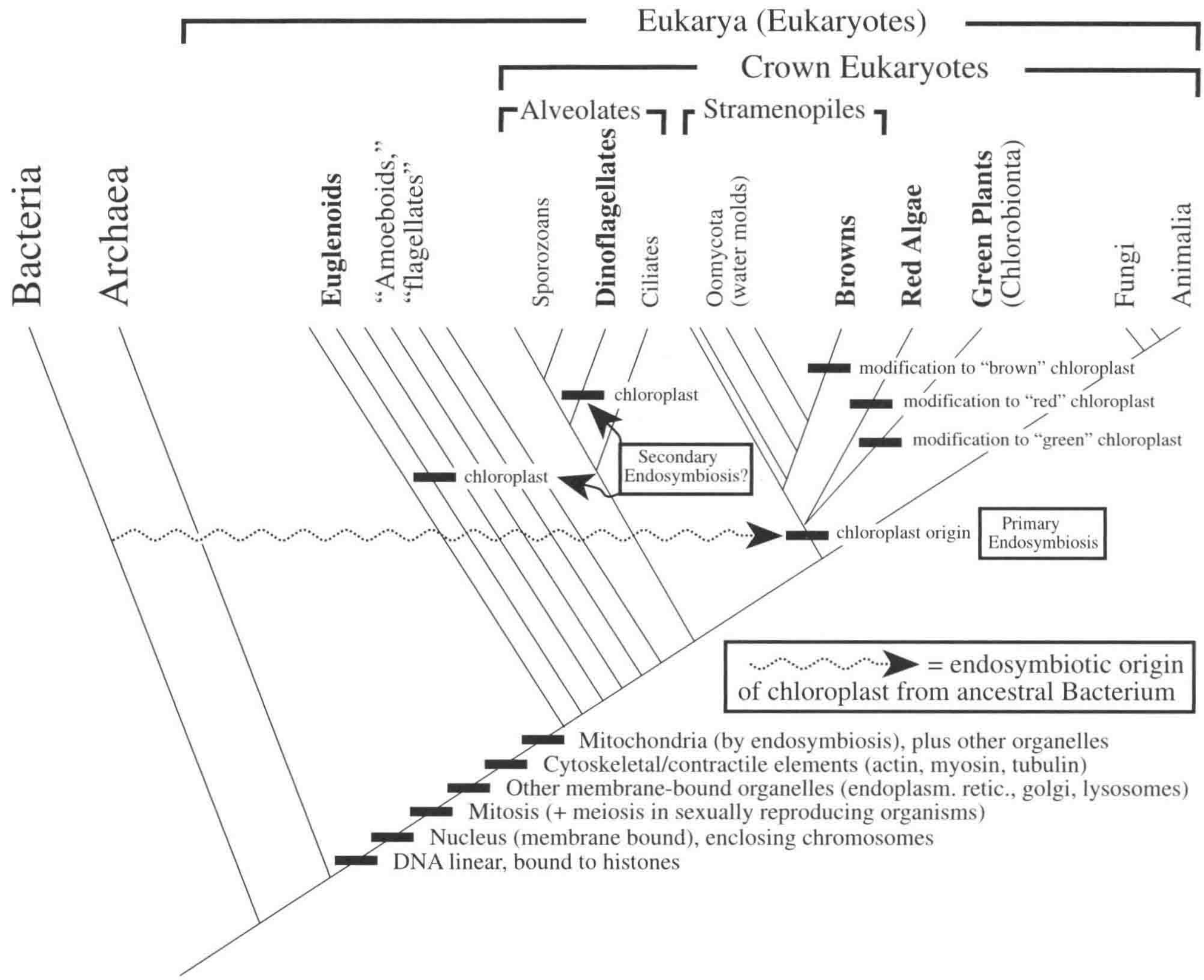


FIGURE 1.1 Simplified cladogram (evolutionary tree) of life (modified from Sogin 1994, Kumar & Rzhetsky 1996, and Yoon et al. 2002), illustrating the independent origin of chloroplasts via endosymbiosis (arrows) in the euglenoids, dinoflagellates, brown plants, red algae, and green plants. Eukaryotic groups containing photosynthetic, chloroplast-containing organisms in bold. The relative order of evolutionary events is unknown.

Some of the unicellular bacteria (including, e.g., the Cyanobacteria, or blue-greens) carry on photosynthesis, a biochemical system in which light energy is used to synthesize high-energy compounds from simpler starting compounds, carbon dioxide and water. These photosynthetic bacteria have a system of internal membranes called thylakoids, within which are embedded photosynthetic pigments, compounds that convert light energy to chemical energy. Of the several groups of eukaryotes that are photosynthetic, all have specialized photosynthetic organelles called **chloroplasts**, which resemble photosynthetic bacteria in having pigment-containing thylakoid membranes.

How did chloroplasts evolve? It is now largely accepted that the chloroplasts of eukaryotes originated by the engulfment of an ancestral photosynthetic bacterium (probably a cyanobacterium) by an ancestral eukaryotic cell, such that the photosynthetic bacterium continued to live and ultimately multiply *inside* the eukaryotic cell (Figure 1.2). The evidence for this is the fact that chloroplasts, like bacteria today (a) have their own single-stranded, circular DNA; (b) have a smaller sized, 70S ribosome; and (c) replicate by fission. These engulfed photosynthetic bacteria provided high-energy products to the eukaryotic cell; the "host" eukaryotic cell provided a more beneficial environment for the photosynthetic bacteria. The condition of two species living together in close contact is termed symbiosis, and the process in which symbiosis results by the engulfment of one cell by another is termed **endosymbiosis**. Over time, these endosymbiotic, photosynthetic bacteria became transformed structurally and functionally, retaining their own DNA and

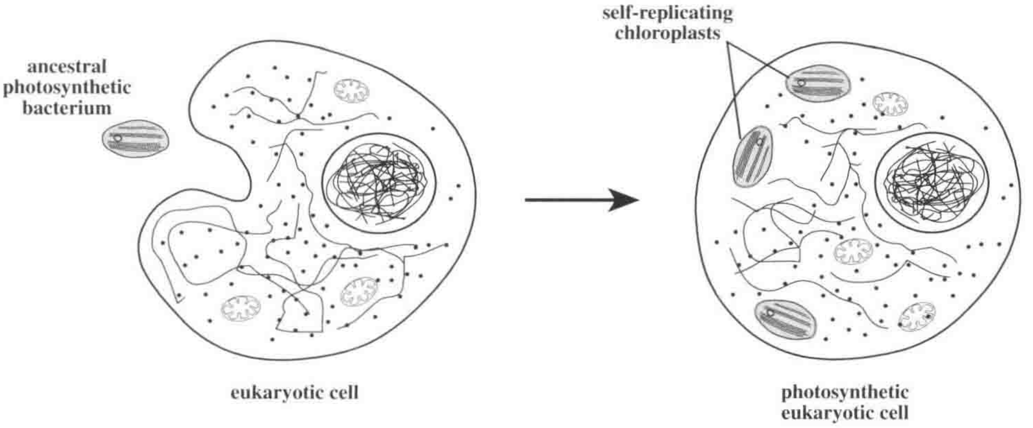


FIGURE 1.2 Diagrammatic illustration of the origin of chloroplasts by endosymbiosis of ancestral photosynthetic bacterium within ancestral eukaryotic cell.

the ability to replicate, but losing the ability to live independently of the host cell. In fact, over time there has been a transfer of some genes from the DNA of the chloroplast to the nuclear DNA of the eukaryotic host cell, making the two biochemically interdependent.

The most recent data from molecular systematic studies indicates that this so-called "primary" endosymbiosis of the chloroplast likely occurred one time, a shared evolutionary novelty of the red algae, green plants, and stramenopiles (which include the brown algae and relatives; Figure 1.1). This early chloroplast became modified with regard to photosynthetic pigments, thylakoid structure, and storage products into forms characteristic of the red algae, green plants, and browns (see Figure 1.1). In addition, chloroplasts may have been lost in some lineages, e.g., in the Oomycota (water molds) of the Stramenopiles. Some lineages of these groups may have acquired chloroplasts via "secondary" endosymbiosis, which occurred by the engulfment of an ancestral chloroplast-containing *eukaryote* by another eukaryotic cell. The euglenoids and the dinoflagellates, two other lineages of photosynthetic organisms, may have acquired chloroplasts by this process (Figure 1.1). The final story is yet to be elucidated.

LAND PLANTS

Of the major groups of photosynthetic eukaryotes, the green plants (also called the Chlorobionta) are united primarily by distinctive characteristics of the green plant chloroplast with respect to photosynthetic pigments, thylakoid structure, and storage compounds (see Chapter 3 for details). Green plants include both the predominately aquatic "green algae" and a group known as embryophytes (formally, the Embryophyta), usually referred to as the land plants (Figure 1.3). The land plants are united by several evolutionary novelties that were adaptations to making the transition from an aquatic environment to living on land. These include (1) an outer cuticle, which aids in protecting tissues from desiccation; (2) specialized gametangia (egg and sperm producing organs) that have an outer, protective layer of sterile cells; and (3) an intercalated diploid phase in the life cycle, the early, immature component of which is termed the embryo (hence, "embryophytes"; see Chapter 3 for details).

Just as the green plants include the land plants, the land plants are inclusive of the vascular plants (Figure 1.3), the latter being united by the evolution of an independent sporophyte and xylem and phloem vascular conductive tissue (see Chapter 4). The vascular plants are inclusive of the seed plants (Figure 1.3), which are united by the evolution of wood and seeds (see Chapter 5). Finally, seed plants include the angiosperms (Figure 1.3), united by the evolution of the flower, including carpels and stamens, and by a number of other specialized features (see Chapters 6–8).

For the remainder of this book, the term *plant* is treated as equivalent to the embryophytes, the land plants. The rationale for this is partly that land plants make up a so-called "natural," monophyletic group, whereas the photosynthetic eukaryotes as a whole are an "unnatural," paraphyletic group (see section on **Phylogeny**, Chapter 2). And, practically, it is land plants that most people are talking about when they refer to "plants," including those in the field of plant systematics. However, as noted before, the word *plant* can be used by some to refer to other groupings; when in doubt, get a precise clarification.

WHY STUDY PLANTS?

The tremendous importance of plants cannot be overstated. Without them, we and most other species of animals (and zof many other groups of organisms) wouldn't be here. Photosynthesis in plants and the other photosynthetic organisms changed the earth in two major ways. First, the fixation of carbon dioxide and the release of molecular oxygen in photosynthesis directly altered the earth's atmosphere over

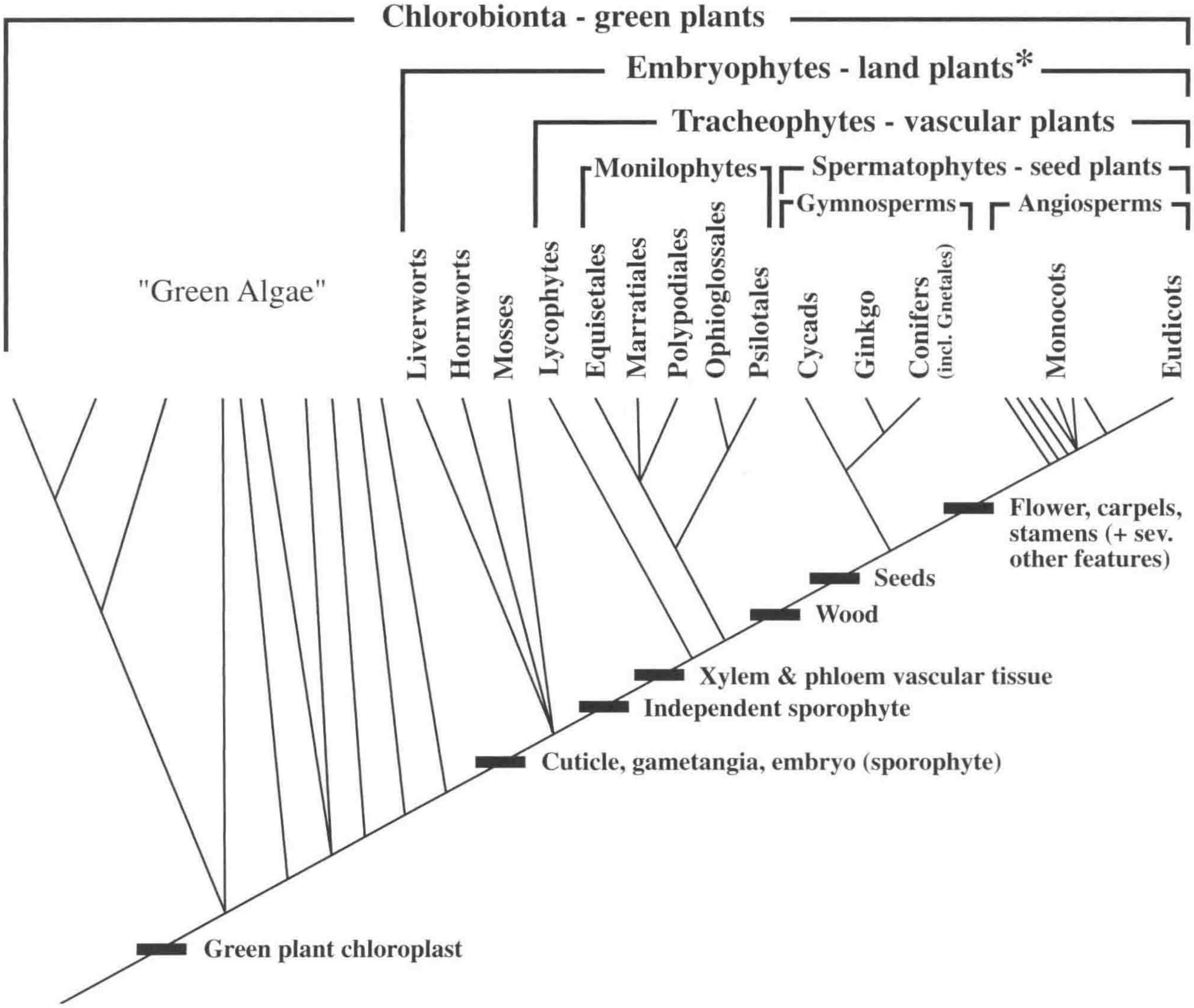


FIGURE 1.3 Simplified cladogram (evolutionary tree) of the green plants, illustrating major extant groups and evolutionary events (or "apomorphies," hash marks). *Embryophytes are treated as "plants" in this book.

billions of years. What used to be an atmosphere deficient in oxygen underwent a gradual change. As a critical mass of oxygen accumulated in the atmosphere, selection for oxygen-dependent respiration occurred (via oxidative phosphorylation in mitochondria), which may have been a necessary precursor in the evolution of many multicellular organisms, including all animals. In addition, an oxygen-rich atmosphere permitted the establishment of an upper atmosphere ozone layer, which shielded life from excess UV radiation. This allowed organisms to inhabit more exposed niches that were previously inaccessible.

Second, the compounds that photosynthetic species produce are utilized, directly or indirectly, by nonphotosynthetic, heterotrophic organisms. For virtually all land creatures and many aquatic ones as well, land plants make up the so-called primary producers in the food chain, the source of high-energy compounds such as carbohydrates, structural compounds such as certain amino acids, and other compounds essential to metabolism in some heterotrophs. Thus, most species on land today, including millions of species of animals, are absolutely dependent on plants for their survival. As primary producers, plants are the major components of many communities and ecosystems. The survival of plants is essential to maintaining the health of those ecosystems, the severe disruption of which could bring about rampant species extirpation or extinction and disastrous changes in erosion, water flow, and ultimately climate.

To humans, plants are also monumentally important in numerous, direct ways (Figures 1.4, 1.5). Agricultural plants,

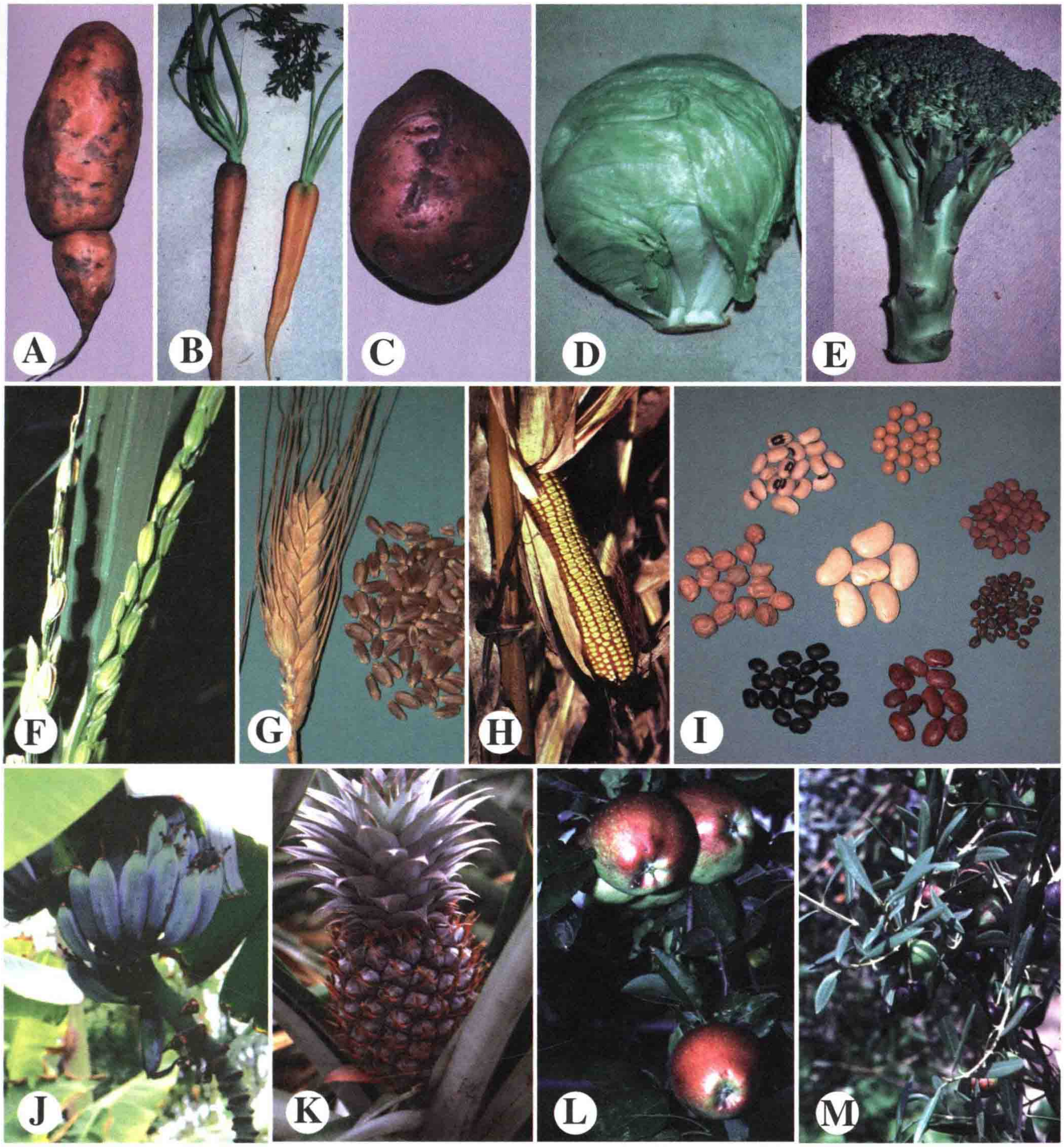


FIGURE 1.4 Examples of economically important plants. **A–E.** Vegetables. **A.** *Ipomoea batatas*, sweet potato (root). **B.** *Daucus carota*, carrot (root). **C.** *Solanum tuberosum*, potato (stem). **D.** *Lactuca sativa*, lettuce (leaves). **E.** *Brassica oleracea*, broccoli (flower buds). **F–I.** Fruits, dry (grains). **F.** *Oryza sativa*, rice. **G.** *Triticum aestivum*, bread wheat. **H.** *Zea mays*, corn. **I.** Seeds (pulse legumes), from top, clockwise to center: *Glycine max*, soybean; *Lens culinaris*, lentil; *Phaseolus aureus*, mung bean; *Phaseolus vulgaris*, pinto bean; *Phaseolus vulgaris*, black bean; *Cicer areitinum*, chick-pea/garbanzo bean; *Vigna unguiculata*, black-eyed pea; *Phaseolus lunatus*, lima bean. **J–M.** Fruits, fleshy. **J.** *Musa paradisiaca*, banana. **K.** *Ananas comosus*, pineapple. **L.** *Malus pumila*, apple. **M.** *Olea europaea*, olive.