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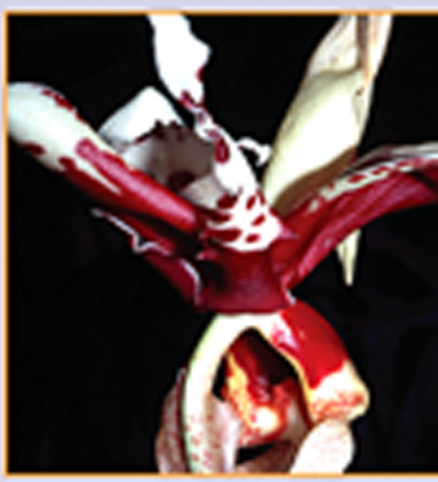

Michael G. Simpson

PLANT SYSTEMATICS

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Michael G. Simpson

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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.

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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 adapti ve 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**hy, 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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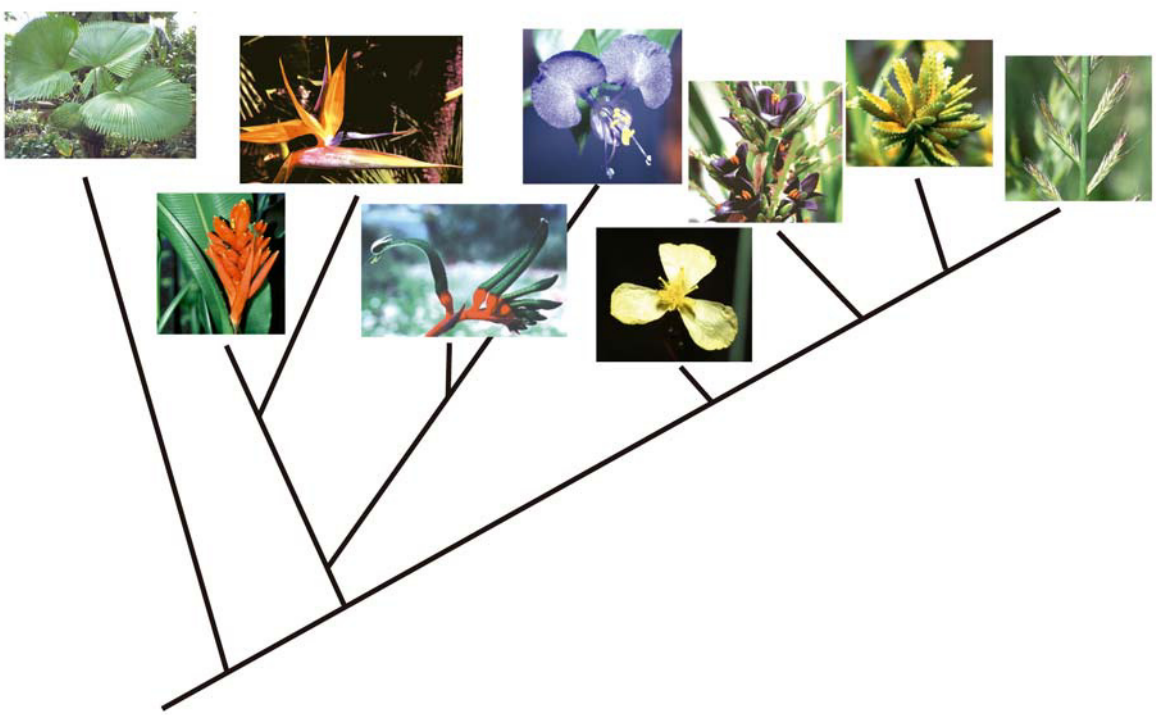
SYSTEMATICS



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PLANT SYSTEMATICS: AN OVERVIEW

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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).

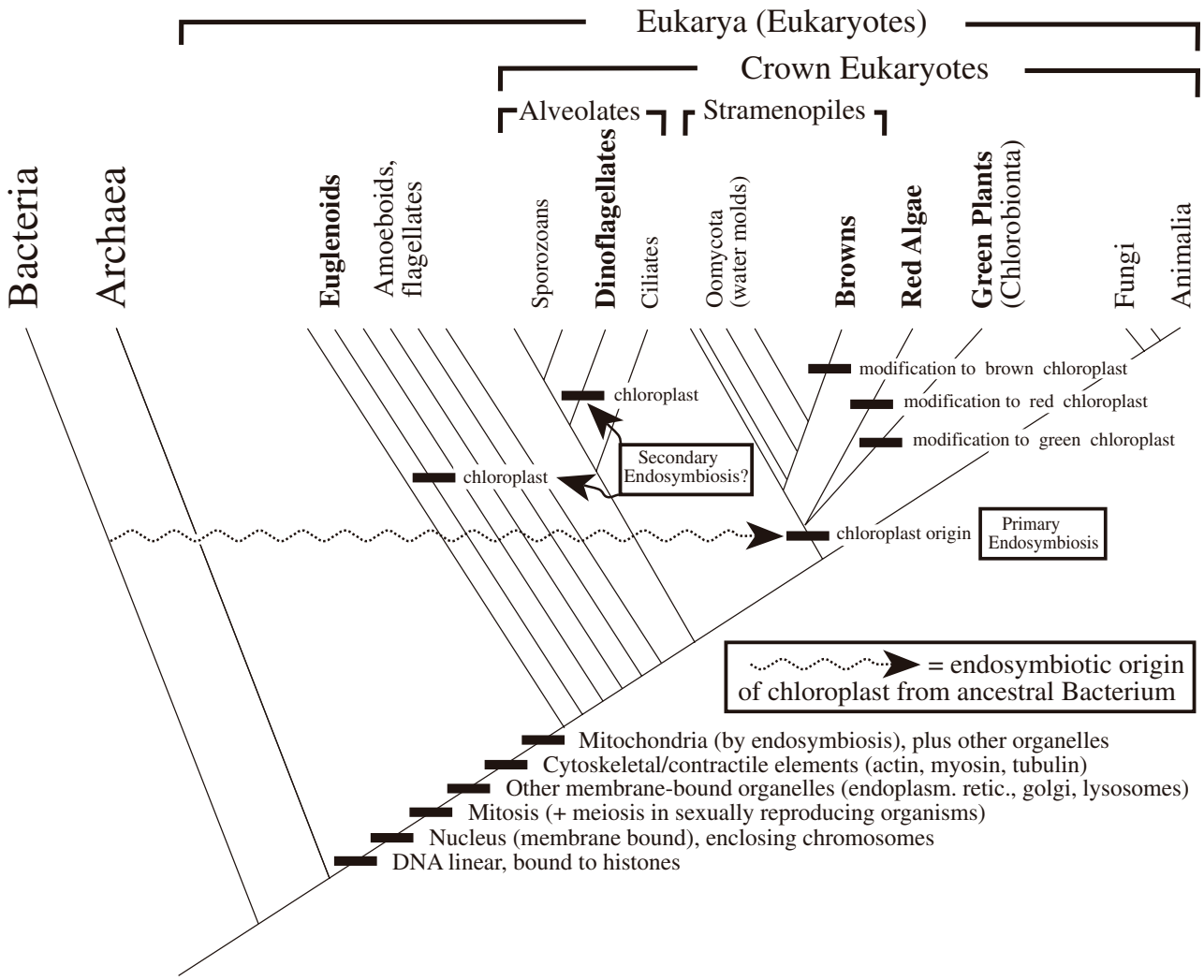

FIGURE 1.1 Simpli ed cladogram (evolutionary tree) of life (modi ed from Sogin 1994, Kumar & Rzhetsky 1996, and Yoon et al. 2002), illustrating the independent origin of chloroplasts via endosymbiosis (arrows) in the euglenoids, dino agellates, brown plants, red algae, and green plants. Eukaryotic groups 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 ssion. These engulfed photosynthetic bacteria provided high-energy products to the eukaryotic cell; the host eukaryotic cell provided a more bene cial 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

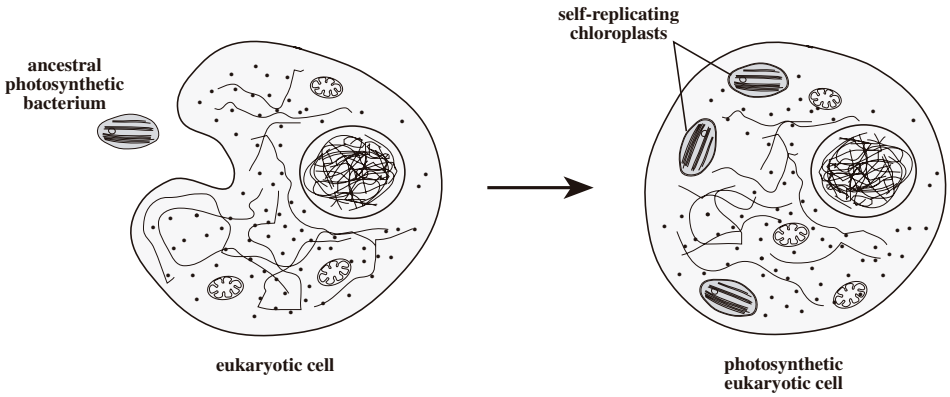

FIGURE 1.2 Diagrammatic illustration of the origin of chloroplasts by endosymbiosis of ancestral photosynthetic bacterium within ancestral eukaryotic cell.

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 modi ed 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 dino agellates, two other lineages of photosynthetic organisms, may have acquired chloroplasts by this process (Figure 1.1). The nal 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 ower, 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 eld 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 clari cation.

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 xation of carbon dioxide and the release of molecular oxygen in photosynthesis directly altered the earth s atmosphere over

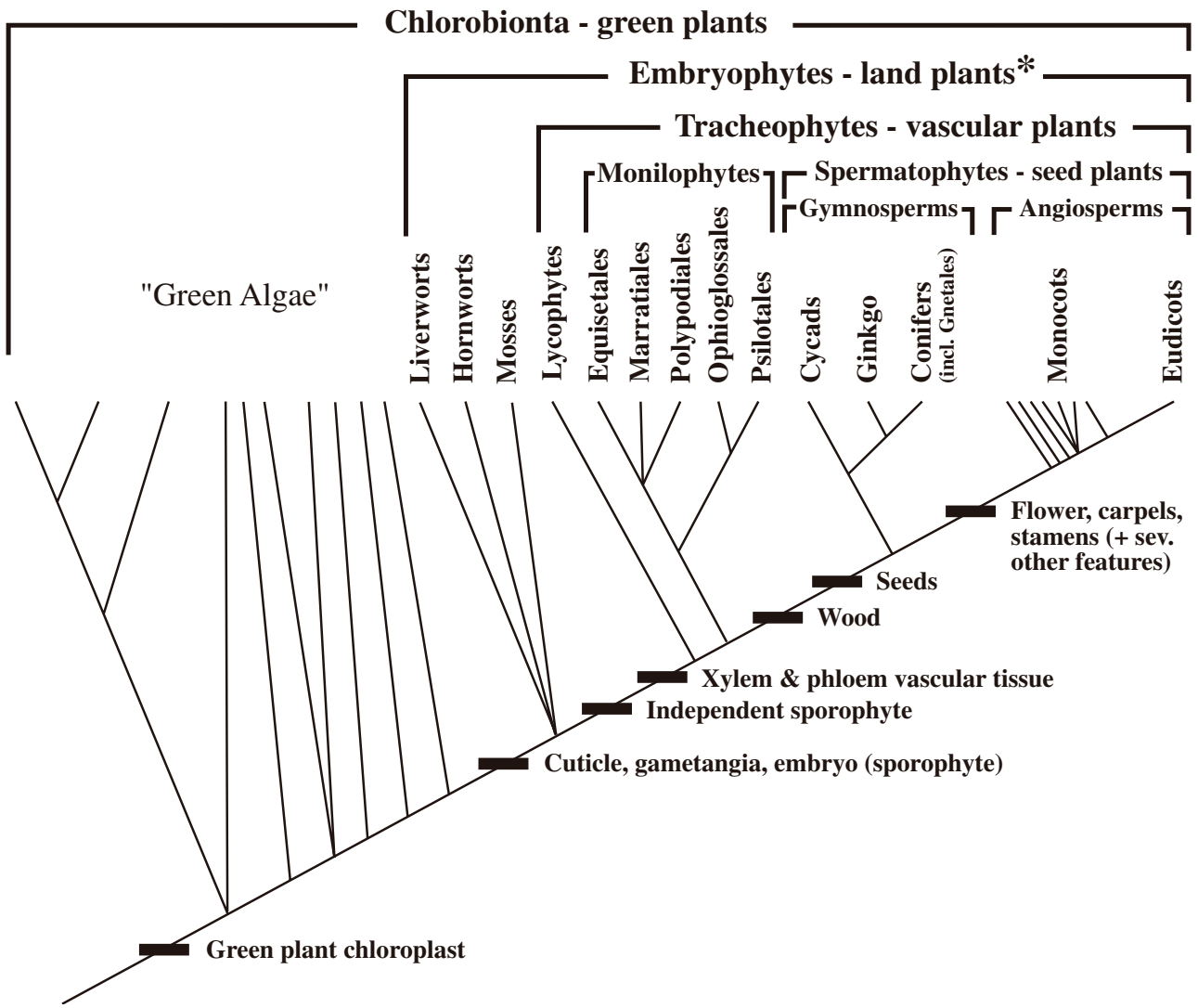

FIGURE 1.3 Simpli ed cladogram (evolutionary tree) of the green plants, illustrating major extant groups and evolutionary events (or apomorphies, hash marks). *Embryophytes are treated as plants in this book.

billions of years. What used to be an atmosphere de cient 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 ow, and ultimately climate.

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

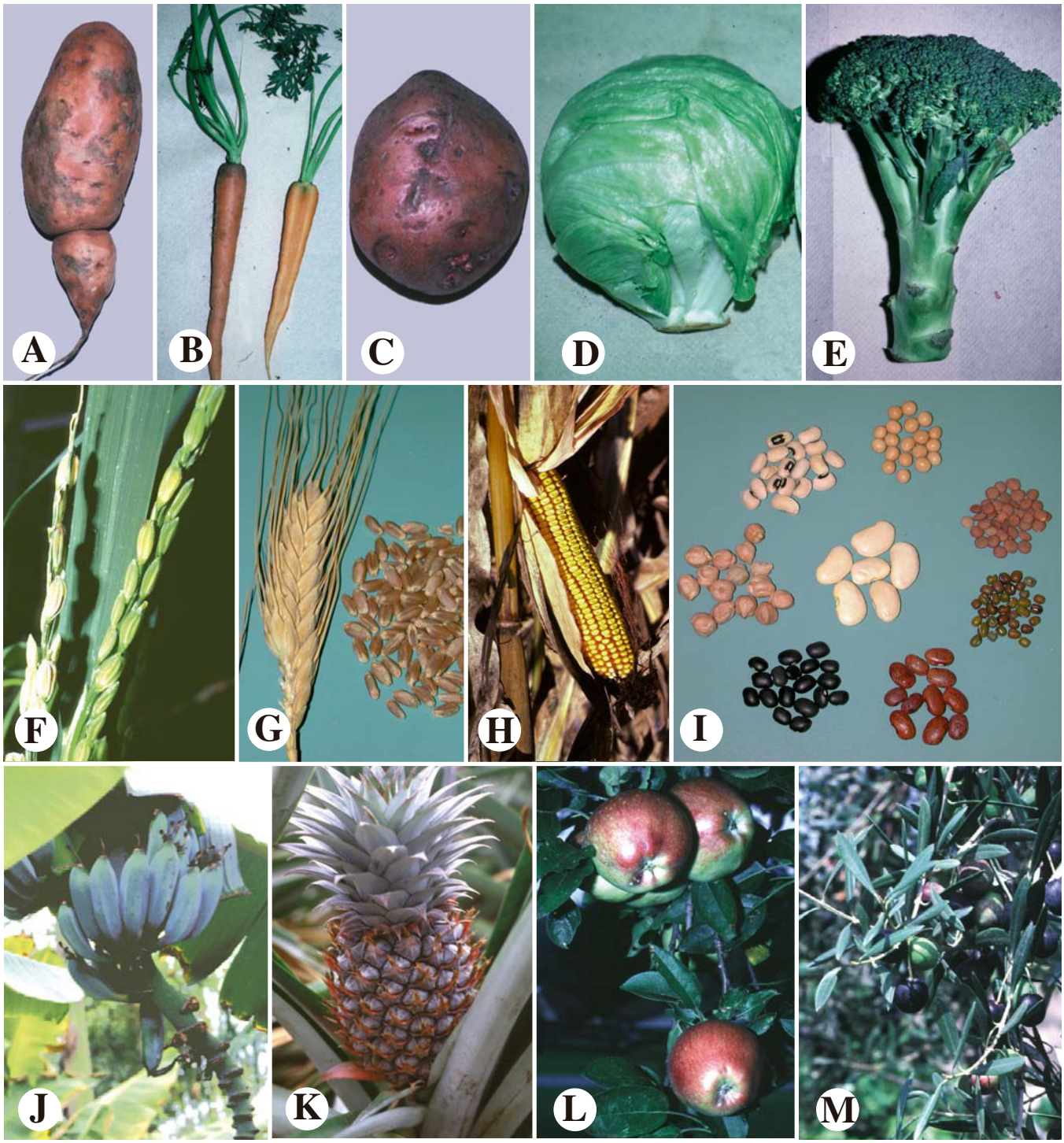

FIGURE 1.4 Examples of economically important plants. **A–E.** Vegetables. **A.** *Ipomoea batatas*, sweet potato (root). **B.** *Daucus carota*, carrot (root). **C.** *Solanum tuberosum*, potato (stem). **D.** *Lactuca sativa*, lettuce (leaves). **E.** *Brassica oleracea*, broccoli (ower buds). **F–I.** 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, eshy. **J.** *Musa paradisiaca*, banana. **K.** *Ananas comosus*, pineapple. **L.** *Malus pumila*, apple. **M.** *Olea europaea*, olive.

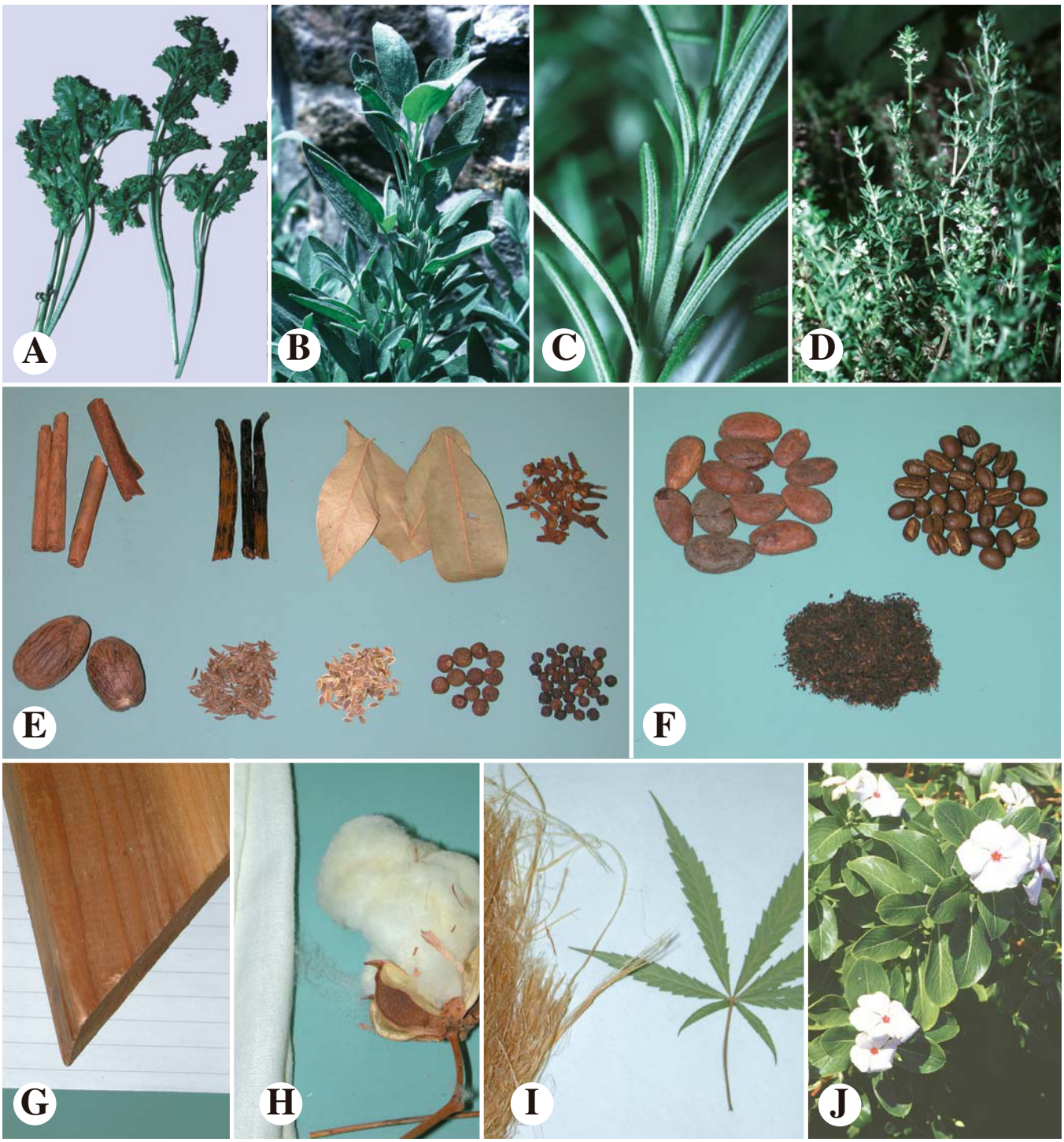

FIGURE 1.5 Further examples of economically important plants. **A–D.** Herbs. **A.** *Petroselinum crispum*, parsley. **B.** *Salvia of cinalis*, sage. **C.** *Rosmarinus of cinalis*, rosemary. **D.** *Thymus vulgaris*, thyme. **E.** Spices and herbs, from upper left: *Cinnamomum cassia/zeylanicum*, cinnamon (bark);*Vanilla planifolia*; vanilla (fruit); *Laurus nobilis*, laurel (leaf); *Syzygium aromaticum*, cloves (ower buds); *Myristica fragrans*, nutmeg (seed); *Carum carvi*, caraway (fruit); *Anethum graveolens*, dill (fruit); *Pimenta dioica*, allspice (seed); *Piper nigrum*, pepper (seed). **F.** Flavoring plants, from upper left, clockwise. *Theobroma cacao*, chocolate (seeds); *Coffea arabica*, coffee (seeds); *Thea sinensis*, tea (leaves). **G.** Wood products: lumber (*Sequoia sempervirens*, redwood), and paper derived from wood pulp. **H.** Fiber plant. *Gossypium* sp., cotton (seed trichomes), one of the most important natural bers. **I.** Euphoric, medicinal, and ber plant. *Cannibis sativa*, marijuana, hemp; stem bers used in twine, rope, and cloth; resins contain the euphoric and medicinal compound tetrahydrocannibinol. **J.** Medicinal plant. *Catharanthus roseus*, Madagascar periwinkle, from which is derived vincristine and vinblastine, used to treat childhood leukemia.

most of which are owering plants, are our major source of food. We utilize all plant parts as food products: roots (e.g., sweet potatoes and carrots; Figure 1.4A,B); stems (e.g., yams, cassava/manioc, potatoes; Figure 1.4C); leaves (e.g., cabbage, celery, lettuce; Figure 1.4D); owers (e.g., cauli ower and broccoli; Figure 1.4E); and fruits and seeds, including grains such as rice (Figure 1.4F), wheat (Figure 1.4G), corn (Figure 1.4H), rye, barley, and oats, legumes such as beans and peas (Figure 1.4I), and a plethora of fruits such as bananas (Figure 1.4J), tomatoes, peppers, pineapples (Figure 1.4K), apples (Figure 1.4L), cherries, peaches, melons, kiwis, citrus, olives (Figure 1.4M), and others too numerous to mention. Other plants are used as avoring agents, such as herbs (Figure 1.5A D) and spices (Figure 1.5E), as stimulating beverages, such as chocolate, coffee, tea, and cola (Figure 1.5F), or as alcoholic drinks, such as beer, wine, distilled liquors, and sweet liqueurs. Woody trees of both conifers and owering plants are used structurally for lumber and for pulp products such as paper (Figure 1.5G). In tropical regions, bamboos, palms, and a variety of other species serve in the construction of human dwellings. Plant bers are used to make thread for cordage (such as sisal), for sacs (such as jute for burlap), and for textiles (most notably cotton, Figure 1.5H, but also linen and hemp, Figure 1.5I). In many cultures, plants or plant products are used as euphorics or hallucinogenics (whether legally or illegally), such as marijuana (Figure 1.5I), opium, cocaine, and a great variety of other species that have been used by indigenous peoples for centuries. Plants are important for their aesthetic beauty, and the cultivation of plants as ornamentals is an important industry. Finally, plants have great medicinal signi cance, to treat a variety of illnesses or to maintain good health. Plant products are very important in the pharmaceutical industry; their compounds are extracted, semisynthesized, or used as templates to synthesize new drugs. Many modern drugs, from aspirin (originally derived from the bark of willow trees) to vincristine and vinblastine (obtained from the Madagascar periwinkle, used to treat childhood leukemia; Figure 1.5J), are ultimately derived from plants. In addition, various plant parts of a great number of species are used whole or are processed as so-called herbal supplements, which have become tremendously popular recently.

The people, methods, and rationale concerned with the **plant sciences** (de ned here as the study of land plants) are as diverse as are the uses and importance of plants. Some of the elds in the plant sciences are very practically oriented. Agriculture and horticulture deal with improving the yield or disease resistance of food crops or cultivated ornamental plants, e.g., through breeding studies and identifying new cultivars. Forestry is concerned with the cultivation and harvesting of trees used for lumber and pulp. Pharmacognosy deals with crude natural drugs, often of plant origin. In contrast to these more practical elds of the plant sciences, the pure sciences ha ve as their goal the advancement of scienti c knowledge (understanding how nature works) through research, regardless of the practical implications. But many aspects of the pure sciences also have important practical applications, either directly by applicable discovery or indirectly by providing the foundation of knowledge used in the more practical sciences. Among these are plant anatomy, dealing with cell and tissue structure and development; plant chemistry and physiology, dealing with biochemical and biophysical processes and products; plant molecular biology, dealing with the structure and function of genetic material; plant ecology, dealing with interactions of plants with their environment; and, of course, plant systematics.

Note that a distinction should be made between botan y and plant sciences. **Plant sciences** is the study of plants, treated as equivalent to land plants here. **Botany** is the study of most organisms traditionally treated as plants, including virtually all eukaryotic photosynthetic organisms (land plants and the several groups of algae) plus other eukaryotic organisms with cell walls and spores (true fungi and groups that were formerly treated as fungi, such as the Oomycota and slime molds). Thus, in this sense, botany is inclusive of but broader than the plant sciences. Recognition of both botany and plant sciences as elds of study can be useful, although how these elds are de ned can vary and may require clari cation.

SYSTEMATICS

WHAT IS SYSTEMATICS?

Systematics is de ned in this book as a science that includes and encompasses traditional **taxonomy**, the description, identi cation, nomenclature, and classi cation of organisms, and that has as its primary goal the reconstruction of **phylogeny**, or evolutionary history, of life. This de nition of *systematics* is not novel, but neither is it universal. Others in the eld would treat taxonomy and systematics as separate but overlapping areas; still others argue that historical usage necessitates what is in essence a reversal of the de nitions used here. But words, like organisms, evolve. The use of *systematics* to describe an all-encompassing eld of endeavor is both most useful and represents the consensus of how most specialists in the eld use the term, an example being the journal *Systematic Botany*, which contains articles both in traditional taxonomy and phylogenetic reconstruction. Plant systematics is studied by acquiring, analyzing, and synthesizing information about plants and

plant parts, the content and methodology of which is the topic for the remainder of this book.

Systematics is founded in the principles of **evolution**, its major premise being that there is one phylogeny of life. The goal of systematists is, in part, to discover that phylogeny.

EVOLUTION

Evolution, in the broadest sense, means change and can be viewed as the cumulative changes occurring since the origin of the universe some 15 billion years ago. Biological evolution, the evolution of life, may be defined (as it was by Charles Darwin) as descent with modification. **Descent** is the transfer of genetic material (enclosed within a cell, the unit of life) from parent(s) to offspring over time. This is a simple concept, but one that is important to grasp and ponder thoroughly. Since the time that life first originated some 3.8 billion years ago, *all life has been derived from preexisting life*. Organisms come to exist by the transfer of genetic material, within a surrounding cell, from one or more parents. Descent may occur by simple clonal reproduction, such as a single bacterial cell parent dividing by fission to form two offspring cells or a land plant giving rise to a vegetative propagule. It may also occur by complex sexual reproduction (Figure 1.6A), in which each of two parents produces specialized gametes (e.g., sperm and egg cells), each of which has half the complement of genetic material, the result of meiosis. Two of the gametes fuse together to form a new cell, the zygote, which may develop into a new individual or may itself divide by meiosis to form gametes. Descent through time results in the formation of a **lineage**, or **clade** (Figure 1.6B,C), a set of organisms interconnected through time and space by the transfer of genetic material from parents to offspring. So, in a very literal sense, we and all other forms of life on earth are connected in time and in space by descent, the transfer of DNA (actually the pattern of DNA) from parent to offspring (ancestor to descendant), generation after generation.

The **modification** component of evolution refers to a change in the genetic material that is transferred from parent(s) to offspring, such that the genetic material of the offspring is different from that of the parent(s). This modification may occur either by mutation, which is a direct alteration of DNA, or by genetic recombination, whereby existing genes are reshuffled in different combinations (during meiosis, by crossing over and independent assortment). Systematics is concerned with the identification of the unique modifications of evolution (see later discussion).

It should also be asked, *what* evolves? Although genetic modification may occur in offspring relative to their parents, individual organisms do not generally evolve. This is because a new individual begins when it receives its complement of DNA from the parent(s); that individual's DNA does not change during its/his/her lifetime (with the exception of relatively rare, nonreproductive somatic mutations that cannot be transmitted to the next generation). The general units of evolution are populations and species. A **population** is a group of individuals of the same species that is usually geographically delimited and that typically have a significant amount of gene exchange. **Species** may be defined in a number of ways, one definition being a distinct lineage that, in sexually reproducing organisms, consists of a group of generally intergrading, interbreeding populations that are essentially reproductively isolated from other such groups. With changes in the genetic makeup of offspring (relative to parents), the genetic makeup of populations and species changes over time.

In summary, evolution is descent with modification occurring by a change in the genetic makeup (DNA) of populations or species over time. How does evolution occur? Evolutionary change may come about by two major mechanisms: (1) **genetic drift**, in which genetic modification is random; or (2) **natural selection**, in which genetic change is directed and nonrandom. Natural selection is the differential contribution of genetic material from one generation to the next, differential in the sense that genetic components of the population or species are contributed in different amounts to the next generation; those genetic combinations resulting in *increased survival or reproduction* are contributed to a greater degree. (A quantitative measure of this differential contribution is known as **fitness**.) Natural selection results in an **adaptation**, a structure or feature that performs a particular function and which itself brings about increased survival or reproduction. In a consideration of the evolution of any feature in systematics, the possible adaptive significance of that feature should be explored.

Finally, an ultimate result of evolution is **speciation**, the formation of new species from preexisting species. Speciation can follow lineage divergence, the splitting of one lineage into two, separate lineages (Figure 1.6D). Lineage divergence is itself a means of increasing evolutionary diversity. If two, divergent lineages remain relatively distinct, they may change independently of one another, into what may be designated as separate species.

TAXONOMY

Taxonomy is a major part of systematics that includes four components: **D**escription, **I**dentification, **N**omenclature, and **C**lassification. (Remember the mnemonic device: **DINC**.) The general subjects of study are **taxa** (singular, **taxon**), which are defined or delimited groups of organisms. Ideally, taxa should have a property known as **monophyly** (discussed

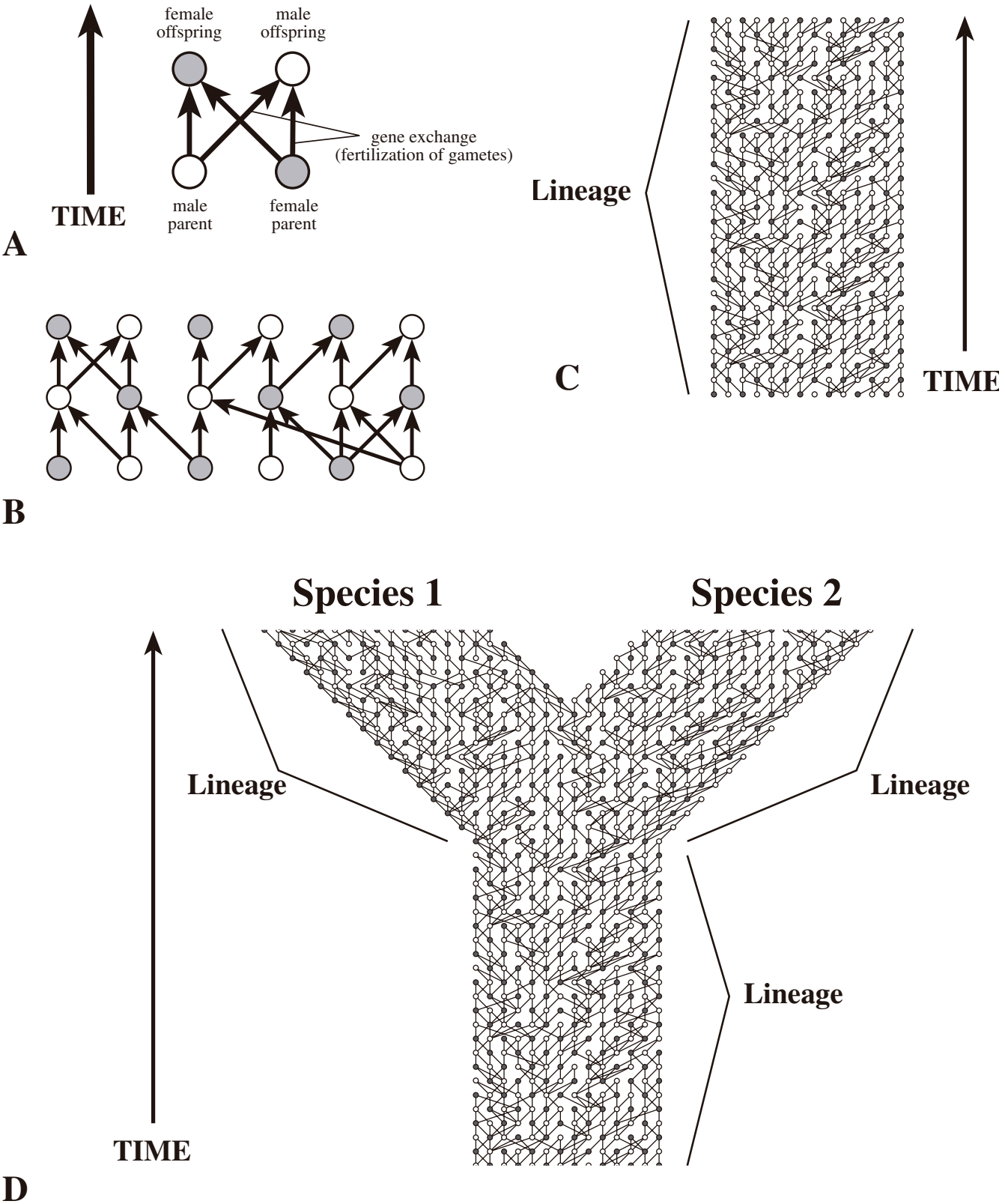

FIGURE 1.6 **A.** Diagram of descent in sexually reproducing species, in which two parents mate to form new offspring. **B.** Gene ow between individuals of a population. **C.** A lineage, the result of gene ow over time. **D.** Divergence of one lineage into two, which may result in speciation (illustrated here).

later; Chapter 2) and are traditionally treated at a particular rank (see later discussion). It should be pointed out that the four components of taxonomy are not limited to formal systematic studies but are the foundation of virtually all intellectual endeavors of all elds, in which conceptual entities are described, identi ed, named, and classi ed. In fact, the ability to describe, identify, name, and classify things undoubtedly has evolved by natural selection in humans and, in part, in other animals as well.

Description is the assignment of features or attributes to a taxon. The features are called **characters**. Two or more forms of a character are **character states**. One example of a character is petal color , for which tw o character states are yello w and blue. Another character is leaf shape, for which possible character states are elliptic, lanceolate, and o vate. Numerous character and character state terms are used in plant systematics, both for general plant morphology (see Chapter 9) and for specialized types of data (Chapters 10 14). The purpose of these descriptive character and character state terms is to use them as tools of communication, for concisely categorizing and delimiting the attributes of a taxon, an organism, or some part of the organism. An accurate and complete listing of these features is one of the major objectives and contributions of taxonomy.

Identi cation is the process of associating an unknown taxon with a known one, or recognizing that the unknown is new to science and warrants formal description and naming. One generally identi es an unknown by rst noting its characteristics, that is, by describing it. Then, these features are compared with those of other taxa to see if they conform. Plant taxa can be identi ed in many ways (see Chapter 15). A taxonomic key is perhaps the most utilized of identi cation devices. Of the different types of taxonomic keys, the most common, used in virtually all oras, is a dichotomous key. A **dichotomous key** consists of a series of two contrasting statements. Each statement is a **lead**; the pair of leads constitutes a **couplet** (Figure 1.7). That lead which best ts the specimen to be identi ed is selected; then all couplets hierarchically beneath that lead (by indentation and/or numbering) are sequentially checked for t until an identi cation is reached (Figure 1.7).

Nomenclature is the formal naming of taxa according to some standardized system. For plants, algae, and fungi, the rules and regulations for the naming of taxa are provided by the International Code of Botanical Nomenclature (see Chapter 16). These formal names are known as **scienti c names**, which by convention are translated into the Latin language. The fundamental principle of nomenclature is that all taxa may bear *only one scienti c name*. Although they may seem dif cult to learn at rst, scienti c names are much preferable to common (vernacular) names (Chapter 16).

The scienti c name of a species traditionally consists of two parts (which are underlined or italicized): the genus name, which is always capitalized, e.g., *Quercus*, plus the speci c epithet, which by recent consensus is not capitalized, e.g., *agrifolia*. Thus, the species name for what is commonly called California live oak is *Quercus agrifolia*. Species names are known as **binomials** (literally meaning tw o names) and this type of nomenclature is called binomial nomenclature, rst formalized in the mid-18th century by Carolus Linnaeus.

Classi cation is the arrangement of entities (in this case, taxa) into some type of order. The purpose of classi cation is to provide a system for cataloguing and expressing relationships between these entities. Taxonomists have traditionally agreed upon a method for classifying organisms that utilizes categories called **ranks**. These taxonomic ranks are hierarchical, meaning that each rank is inclusive of all other ranks beneath it (Figure 1.8).

As de ned earlier, a **taxon** is a group of organisms typically treated at a given rank. Thus, in the example of Figure 1.8, Magnoliophyta is a taxon placed at the rank of phylum; Liliopsida is a taxon placed at the rank of class; Arecaceae is a taxon

		1. Annual; leaves <<1 cm long; owers 1 4 mm	
Couplet:	*Lead:*	2. Leaves opposite, pairs fused around stem; owers axillary; petals <2 mm	*Crassula*
	Lead:	2 Leaves alternate above, free; owers in terminal cyme; petals 1.5 4.5 mm	*Parvisedum*
		1 Generally perennial herbs to shrubs; leaves >1 cm; owers generally >10 mm (if annual, owers >4 mm)	
		3. Shrub or subshrub	
		4. Leaves alternate, many in rosette, ciliate; sepals 6 16; petals ± free	*Aeonium*
		4 Leaves opposite, few, not ciliate; sepals 5; petals fused, tube > sepals	*Cotyledon*
		3 Perennial herb (annual or biennial in *Sedum radiatum*)	
		5. In orescence axillary; cauline leaves different from rosette leaves	*Dudleya*
		5 In orescence terminal; cauline leaves like rosettes, or basal leaves brown, scale-like	*Sedum*

FIGURE 1.7 Dichotomous key to the genera of the Crassulaceae of California, by Reid Moran, ' *The Jepson Manual* (1993, Hickman, ed., University of California Press, Berkeley), reprinted by special permission.

Major Taxonomic Ranks	Taxa
Kingdom	Plantae
Phylum (**Division** also acceptable)	Magnoliophyta
Class	Liliopsida (Monocots)
Order	Arecales
Family	Arecaceae
Genus (plural: genera)	*Cocos*
Species (plural: species)	*Cocos nucifera*

FIGURE 1.8 The primary taxonomic ranks accepted by the International Code of Botanical Nomenclature.

placed at the rank of family; etc. Note that taxa of a particular rank generally end in a particular suf x (Chapter 16). There is a trend among systematic biologists to eliminate the rank system of classi cation (see Chapter 16). In this book, ranks are used for naming groups but not emphasized as ranks.

There are two major means of arriving at a classi cation of life: phenetic and phylogenetic. **Phenetic** classi cation is that based on overall similarities. Most of our everyday classi cations are phenetic. For ef ciency of organization (e.g., storing and retrieving objects, like nuts and bolts in a hardware store) we group similar objects together and dissimilar objects apart. Many traditional classi cations in plant systematics are phenetic, based on noted similarities between and among taxa. **Phylogenetic** classi cation is that which is based on evolutionary history, or pattern of descent, which may or may not correspond to overall similarity (see later discussion, Chapter 2).

PHYLOGENY

Phylogeny, the primary goal of systematics, refers to the evolutionary history of a group of organisms. Phylogeny is commonly represented in the form of a **cladogram** (or phylogenetic tree), a branching diagram that conceptually represents the evolutionary pattern of descent (see Figure 1.9). The lines of a cladogram represent **lineages** or **clades**, which (as discussed earlier) denote descent, the sequence of ancestral-descendant populations through time (Figure 1.9A). Thus, cladograms have an implied (relative) time scale. Any branching of the cladogram represents lineage **divergence**, the diversi cation of lineages from one **common ancestor**.

Changes in the genetic makeup of populations, i.e., evolution, may occur in lineages over time. Evolution may be recognized as a change from a preexisting, or **ancestral**, character state to a new, **derived** character state. The derived character state is an evolutionary novelty, also called an **apomorphy** (Figure 1.9A). **Phylogenetic systematics**, or **cladistics**, is a methodology for inferring the pattern of evolutionary history of a group of organisms, utilizing these apomorphies (Chapter 2).

As cited earlier, cladograms serve as the basis for phylogenetic classi cation. A key component in this classi cation system is the recognition of what are termed monophyletic groups of taxa. A **monophyletic group** is one consisting of a common ancestor plus all (and only all) descendants of that common ancestor. For example, the monophyletic groups of the cladogram in Figure 1.9B are circled. A phylogenetic classi cation recognizes only monophyletic groups. Note that some monophyletic groups are included within others (e.g., in Figure 1.9B the group containing only taxa *E* and *F* is included within the group containing only taxa *D*, *E*, and *F*, which is included within the group containing only taxa *B*, *C*, *D*, *E*, and *F*, etc.). The sequential listing of monophyletic groups can serve as a phylogenetic classi cation scheme (see Chapter 2).

In contrast to a monophyletic group, a **paraphyletic group** is one consisting of a common ancestor but *not all* descendants of that common ancestor; a **polyphyletic group** is one in which there are two or more separate groups, each with a separate common ancestor. Paraphyletic and polyphyletic groups distort the accurate portrayal of evolutionary history and should be abandoned (see Chapter 2).

Knowing the phylogeny of a group, in the form of a cladogram, can be viewed as an important end in itself. As discussed earlier, the cladogram may be used to devise a system of classi cation, one of the primary goals of taxonomy. The cladogram also can be used as a tool for addressing several interesting biological questions, including biogeographic or ecological history, processes of speciation, and adaptive character evolution. A thorough discussion of the principles and methodology of phylogenetic systematics is discussed in Chapter 2.

WHY STUDY SYSTEMATICS?

The rationale and motives for engaging the eld of systematics are worth examining. For one, systematics is important in

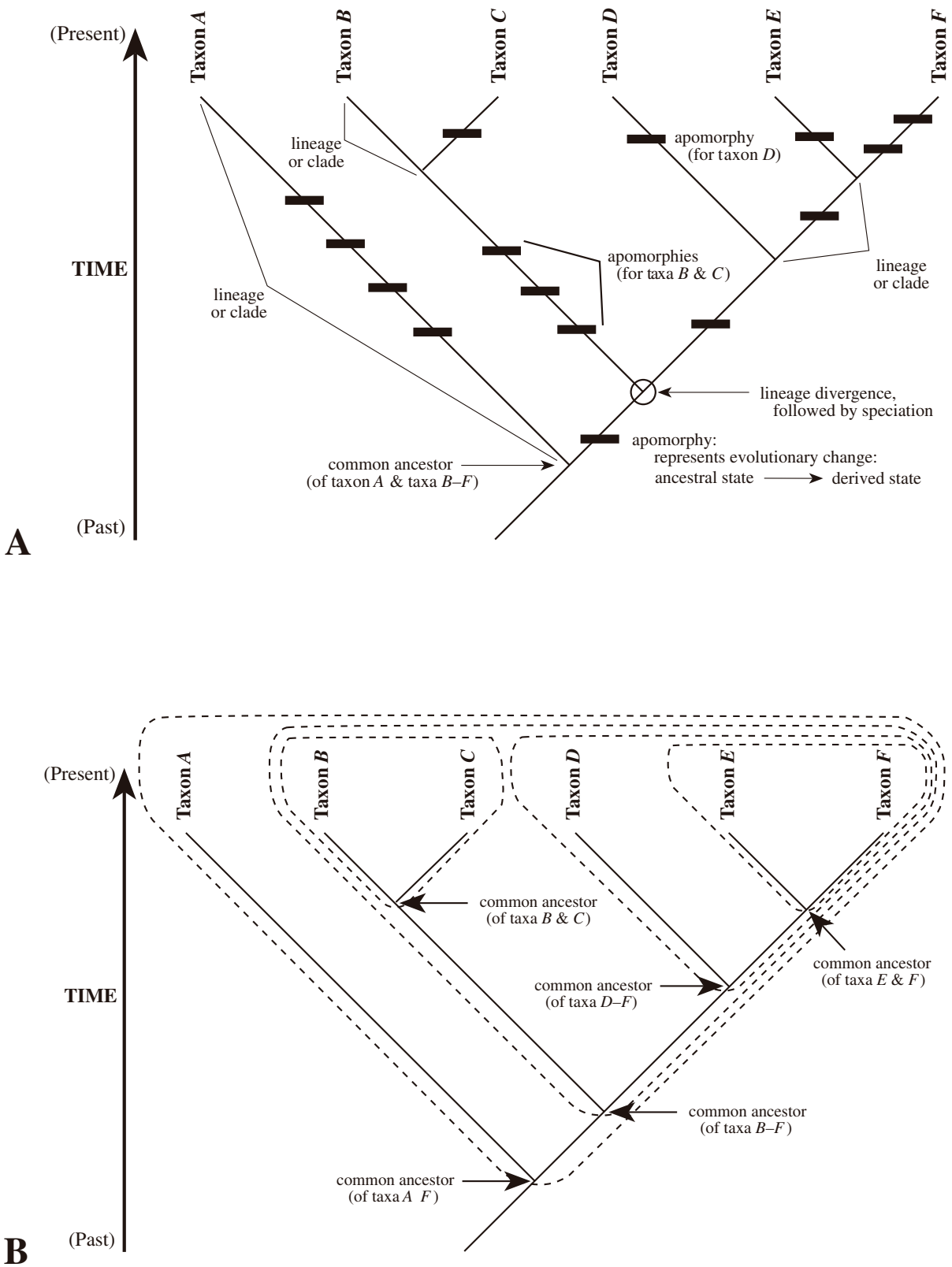

FIGURE 1.9 Example of a cladogram or phylogenetic tree for taxa *A F*. **A.** Cladogram showing lineages and apomorphies, the latter indicated by thick hash marks. **B.** Cladogram with common ancestors shown and monophyletic groups circled.

providing a foundation of information about the tremendous diversity of life. Virtually all fields of biology are dependent on the correct taxonomic determination of a given study organism, which relies on formal description, identification, naming, and classification. Systematic research is the basis for acquiring, cataloguing, and retrieving information about life's diversity. Essential to this research is documentation, through collection (Chapter 17) and storage of reference specimens, e.g., for plants in an accredited herbarium (Chapter 18). Computerized data entry of this collection information is now vital to cataloguing and retrieving the vast amount of information dealing with biodiversity (Chapter 18).

Systematics is also an integrative and unifying science. One of the fun aspects of systematics is that it may utilize data from all fields of biology: morphology, anatomy, embryology/development, ultrastructure, paleontology, ecology, geography, chemistry, physiology, genetics, karyology, and cell/molecular biology. The systematist has an opportunity to understand all aspects of his/her group of interest in an overall synthesis of what is known from all biological specialties, with the goal being to understand the evolutionary history and relationships of the group.

Knowing the phylogeny of life can give insight into other fields and have significant practical value. For example, when a species of *Dioscorea*, wild yam, was discovered to possess steroid compounds (used first in birth control pills), examination of other closely related species revealed species that contained even greater quantities of these compounds. Other examples corroborate the practical importance of knowing phylogenetic relationships among plant species. The methodology of phylogenetics is now an important part of comparative biology, used by, for example, evolutionary ecologists, functional biologists, and parasitologists, all of whom need to take history into account in formulating and testing hypotheses.

The study of systematics provides the scientific basis for defining or delimiting species and infraspecific taxa (subspecies or varieties) and for establishing that these are distinct from other, closely related and similar taxa. Such studies are especially important today in conservation biology. In order to determine whether a species or infraspecific taxon of plant is rare or endangered and warrants protection, one must first know the limits of that species or infraspecific taxon. In addition, understanding the history of evolution and geography may aid in conservation and management decisions, where priorities must be set as to which regions to preserve.

Finally, perhaps the primary motivation for many, if not most, in the field of systematics has been the joy of exploring the intricate complexity and incredible diversity of life. This sense of wonder and amazement about the natural world is worth cultivating (or occasionally rekindling). Systematics also can be a challenging intellectual activity, generally requiring acute and patient skills of observation. Reconstruction of phylogenetic relationships and ascertaining the significance of those relationships can be especially challenging and rewarding. But today we also face a moral issue: the tragic and irrevocable loss of species, particularly accelerated by rampant destruction of habitat, such as deforestation in the tropics. We can all try to help, both on a personal and professional level. Systematics, which has been called simply the study of biodiversity, is *the* major tool for documenting that biodiversity and can be a major tool for helping to save it. Perhaps we can all consider reassessing our own personal priorities in order to help conserve the life that we study.

REVIEW QUESTIONS

PLANTS

1. What is a plant? In what two conceptual ways can the answer to this question be approached?
2. What are the three major groups of life currently accepted?
3. Name and define the mechanism for the evolution of chloroplasts.
4. Name some chlorophyllous organismal groups that have traditionally been called plants but that evolved chloroplasts independently.
5. Draw a simplified cladogram showing the relative relationships among the green plants (Chlorobionta), land plants (embryophytes), vascular plants (tracheophytes), seed plants (spermatophytes), gymnosperms, and angiosperms (flowering plants).
6. Why are land plants treated as equivalent to plants in this book?
7. List the many ways that plants are important, both in the past evolution of life on earth and in terms of direct benefits to humans.

SYSTEMATICS

8. What is systematics and what is its primary emphasis?
9. De ne biological evolution, describing what is meant both by descent and by modi cation.
10. What is a lineage (clade)?
11. Name and de ne the units that undergo evolutionary change.
12. What are the two major mechanisms for evolutionary change?
13. What is a functional feature that results in increased survival or reproduction called?
14. Name and de ne the four components of taxonomy.
15. De ne character and character state.
16. Give one example of a character and character state from morphology or from some type of specialized data.
17. What is a dichotomous key? a couplet? a lead?
18. What is a scienti c name?
19. De ne binomial and indicate what each part of the binomial is called.
20. What is the difference between rank and taxon?
21. What is the plural of taxon?
22. Name the two main ways to classify organisms and describe how they differ.
23. De ne phylogeny and give the name of the branching diagram that represents phylogeny.
24. What does a split, from one lineage to two, represent?
25. Name the term for both a preexisting feature and a new feature.
26. What is phylogenetic systematics (cladistics)?
27. What is a monophyletic group? a paraphyletic group? a polyphyletic group?
28. For what can phylogenetic methods be used?
29. How is systematics the foundation of the biological sciences?
30. How can systematics be viewed as unifying the biological sciences?
31. How is systematics of value in conservation biology?
32. Of what bene t is plant systematics to you?

EXERCISES

1. Obtain de nitions of the word *plant* by asking various people (lay persons or biologists) or looking in reference sources, such as dictionaries or textbooks. Tabulate the various de nitions into classes. What are the advantages and disadvantages of each?
2. Take a day to note and list the uses and importance of plants in your everyday life.
3. Pick a subject, such as history or astronomy, and cite how the principles of taxonomy are used in its study.
4. Do a Web search for a particular plant species (try common and scienti c name) and note what aspect of plant biology each site covers.
5. Peruse ve articles in a systematics journal and tabulate the different types of research questions that are addressed.

REFERENCES FOR FURTHER STUDY

Kumar, S., and A. Rzhetsky. 1996. Evolutionary relationships of eukaryotic kingdoms. Journal of Molecular Evolution 42: 183 193 .

Reaka-Kudla, M. L., D. E. Wilson, and E. O. Wilson (eds.). 1997. Biodiversity II: Understanding and Protecting Our Biological Resources. Joseph Henry Press, Washington, DC.

Simpson, B. B., and M. C. Ogorzaly. 2001. Economic Botany: Plants in Our World. McGraw-Hill, New York.

Sogin, M. L. 1994. The origin of eukaryotes and evolution into major kingdoms. Bengtson, S. (ed.). Nobel Symposium, No. 84. Early life on earth; 84th Nobel Symposium, Karlskoga, Sweden, May 16, 1992. Columbia University Press, New York, pp. 181 192.

Systematics Agenda 2000: Charting the Biosphere. 1994. Produced by Systematics Agenda 2000. [This is an excellent introduction to the goals and rationale of systematic studies, described as a global initiati ve to discover, describe and classify the world s species. A vailable through SA2000, Herbarium, New York Botanical Garden, Bronx, New York 10458, USA]

Wilson, E. O. (ed.), and F. M. Peter (assoc. ed.). 1988. Biodiversity. National Academy Press, Washington, DC.

Yoon, H. S., J. D. Hackett, G. Pinto, and D. Bhattacharya. 2002. The single ancient origin of chromist plastids. Proceedings of the National Academy of Sciences of the United States of America 99: 15507 15512.

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OVERVIEW AND GOALS

As introduced in the previous chapter, **phylogeny** refers to the evolutionary history or pattern of descent of a group of organisms and is one of the primary goals of systematics. **Phylogenetic systematics**, or **cladistics**, is that branch of systematics concerned with inferring phylogeny. Ever since Darwin laid down the fundamental principles of evolutionary theory, one of the major goals of the biological sciences has been the determination of life s history of descent. This phylogeny of organisms, visualized as a branching pattern, can be determined by an analysis of characters from living or fossil organisms, utilizing phylogenetic principles and methodology.

As reviewed in Chapter 1, a phylogeny is commonly represented in the form of a **cladogram**, or **phylogenetic tree**, a branching diagram that conceptually represents the best estimate of phylogeny (Figure 2.1). The lines of a cladogram are known as **lineages** or **clades**. Lineages represent the sequence of ancestral-descendant populations through time, ultimately denoting descent.

Thus, as previously reviewed, cladograms have an implied, but relative, time scale. Any branching of the cladogram represents lineage **divergence** or **diversification**, the formation of two separate lineages from one **common ancestor**. (The two lineages could diverge into what would be designated separate species, the process of forming two species from one termed **speciation**.) The *point* of divergence of one clade into

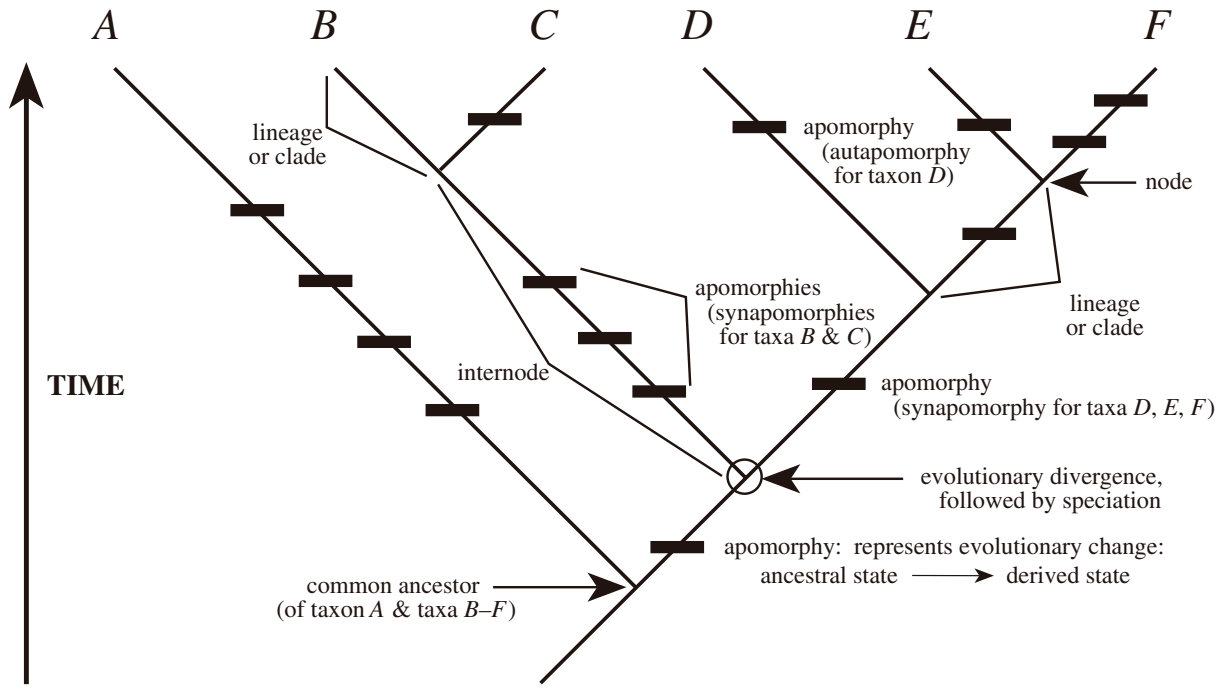

FIGURE 2.1 Example of a cladogram or phylogenetic tree for taxa *A–F*, with apomorphies indicated by thick hash marks; redrawn from Chapter 1. See text for explanation of terms.

two (where the most common ancestor of the two divergent clades is located) is termed a **node**; the region between two nodes is called an **internode** (Figure 2.1).

Evolution may occur within lineages over time and is recognized as a change from a preexisting **ancestral** (also called **plesiomorphic** or **primitive**) condition to a new, **derived** (also called **apomorphic** or **advanced**) condition. The derived condition, or **apomorphy**, represents an evolutionary novelty. As seen in Figure 2.1, an apomorphy that unites two or more lineages is known as a **synapomorphy** (*syn*, together); one that occurs within a single lineage is called an **autapomorphy** (*aut*, self). However, either may be referred to simply as an **apomorphy**, a convention used throughout this book. Cladograms may be represented in different ways. Figure 2.2 shows the same cladogram as in Figure 2.1, but shifted 90° clockwise and with the lineages drawn perpendicular to one another and of a length reflective of the number of apomorphic changes.

Why study phylogeny? Knowing the pattern of descent, in the form of a cladogram, can be viewed as an important end in itself. The branching pattern derived from a phylogenetic analysis may be used to infer the collective evolutionary changes that have occurred in ancestral/descendant populations through time. Thus, a knowledge of phylogenetic relationships may be invaluable in understanding structural evolution as well as in gaining insight into the possible functional, adaptive significance of hypothesized evolutionary changes. The cladogram can also be used to classify life in a way that directly reflects evolutionary history. Cladistic analysis may also serve as a tool for inferring biogeographic and ecological history, assessing evolutionary processes, and making decisions in the conservation of threatened or endangered species.

The principles, methodology, and applications of phylogenetic analyses are described in the remainder of this chapter.

TAXON SELECTION

The study of phylogeny begins with the selection of **taxa** (taxonomic groups) to be analyzed, which may include living and/or fossil organisms. Taxon selection includes both the group as a whole, called the study group or **ingroup**, and the individual unit taxa, termed **O**perational **T**axonomic **U**nits, or **OTUs**. The rationale as to *which* taxa are selected from among many rests by necessity on previous classifications or phylogenetic hypotheses. The ingroup is often a traditionally defined taxon for which there are competing or uncertain classification schemes, the objective being to test the bases of those different classification systems or to provide a new