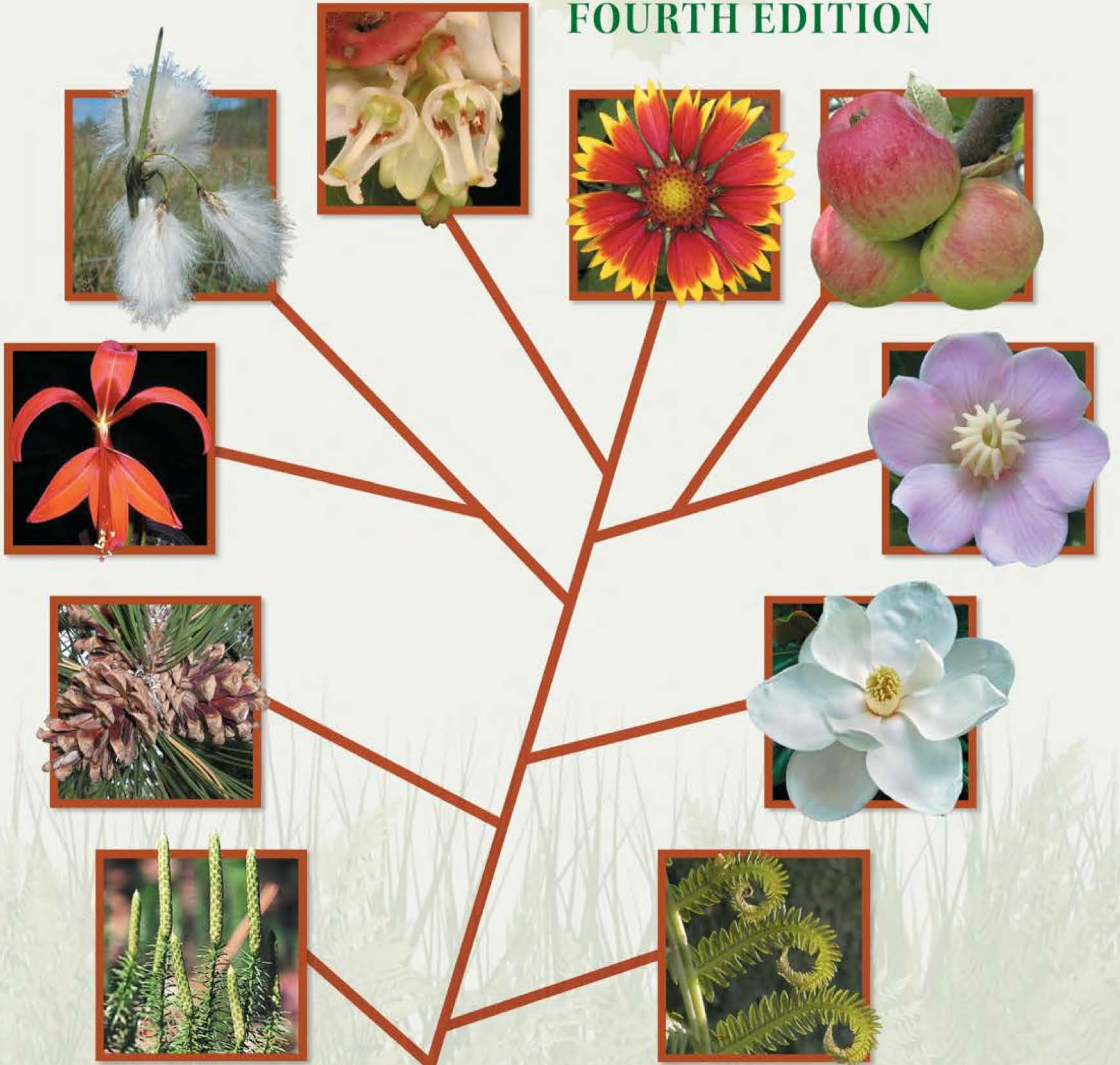


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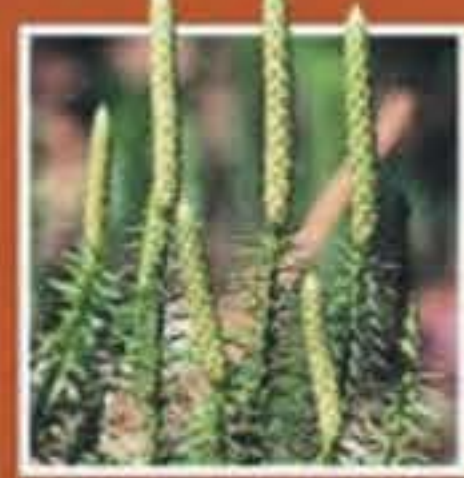
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Plant Systematics

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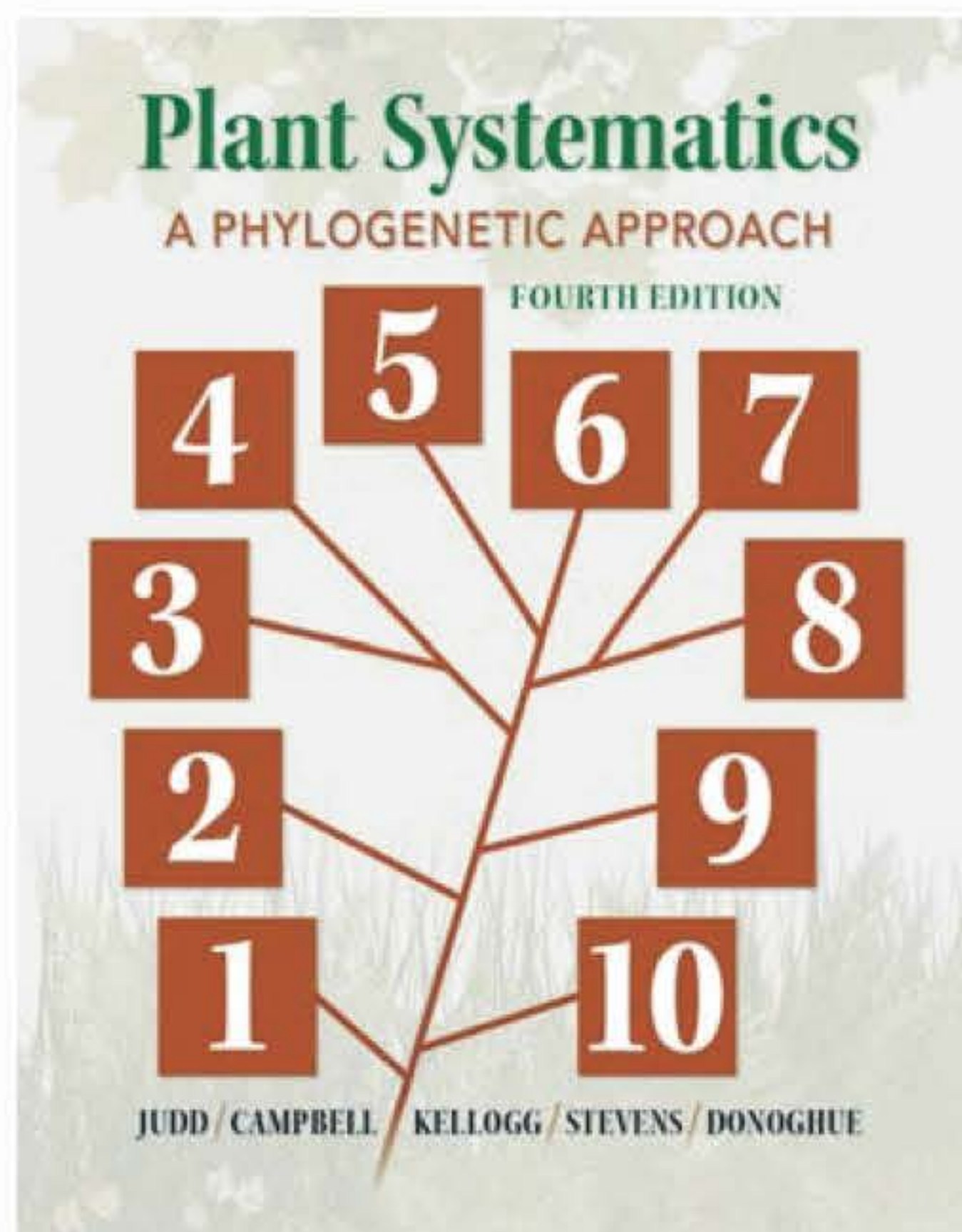
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The Cover

(1) Lycophyte, *Lycopodium annotinum* (Lycopodiaceae). (2) Conifer, *Pinus nigra* (Pinaceae). (3, 4) Monocots: *Sprekelia formosissima* (Amaryllidaceae); *Eriophorum angustifolium* (Cyperaceae). (5, 6) Asterids: *Leucothoe axillaris* (Ericaceae); *Gaillardia pulchella* (Asteraceae). (7, 8) Rosids: *Malus domestica* (Rosaceae); *Blakea gracilis* (Melastomataceae). (9) Magnoliid, *Magnolia grandiflora* (Magnoliaceae). (10) Monilophyte (leptosporangiate fern), *Matteuccia struthiopteris* (Onocleaceae). Photographs of *Eriophorum angustifolium* by Tanja M. Schuster, of *Leucothoe axillaris* by Kurt M. Neubig, of *Blakea gracilis* by Barbara S. Carlswald, of *Magnolia grandiflora* by Dora Modly-Paris (© Shutterstock, used with permission), and of *Matteuccia struthiopteris* by David McIntyre; all others by Walter S. Judd. Background images: sugar maple leaves (top), © Evgeny Sergeev/istock; grasses, ferns, and flowers (bottom), © LillyBeth Filth/TRU Textures Ltd.

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*With appreciation, we dedicate this textbook to our mentor and friend,
the late Carroll E. Wood, Jr.,
whose kindness and knowledge of plant systematics
have helped many students and colleagues.*

Contents in Brief

CHAPTER 1

The Science of Plant Systematics 1

CHAPTER 2

Methods and Principles of Biological Systematics 13

CHAPTER 3

Classification and System in Flowering Plants: Historical Background 49

CHAPTER 4

Taxonomic Evidence: Structural and Biochemical Characters 65

CHAPTER 5

The Evolution of Plant Diversity 119

CHAPTER 6

An Overview of Green Plant Phylogeny 157

CHAPTER 7

Lycophytes, Ferns, and Gymnosperms 193

CHAPTER 8

Phylogenetic Relationships of Angiosperms 237

APPENDIX ONE

Botanical Nomenclature 589

APPENDIX TWO

Specimen Preparation and Identification 601

Contents



CHAPTER 1 The Science of Plant Systematics 1

What Do We Mean by *Plant*? 1

What Do We Mean by *Systematics*? 2

The Phylogenetic Approach 3

How Do We Reconstruct Phylogeny? 3

What Is Monophyly? 5

The Practice of Plant Systematics 6

Why Is Systematics Important? 7

Aims and Organization of This Book 11

Literature Cited & Suggested Readings 12



CHAPTER 2 Methods and Principles of Biological Systematics 13

Discovering Phylogeny: How Phylogenetic Trees Are Constructed 13

Evolutionary Trees and What They Depict:
Reading the Tree 13

Sources of DNA Sequence Data 15

Gene-by-Gene Approaches 16

Genomic Approaches 17

Sequence Alignment 17

Rooting 20

Homoplasy 21

Tree Building: Clustering Algorithms and
Neighbor Joining 23

Models of Evolution 24

Should You Believe the Tree: Bootstrapping
and Comparison of Trees 26

Methods That Use an Optimality Criterion 27

Comparing Trees from Different Methods
and Sources of Data 34

Using Phylogenetic Trees 37

Constructing a Classification 37

Describing Evolution: Mapping Characters
onto Trees 41

Assigning Dates to Nodes in Phylogenies 45

Literature Cited & Suggested Readings 46



CHAPTER 3 Classification and System in Flowering Plants: Historical Background 49

Classification, Nature, and Stability 50

Botany, Classification, and Biology 51

Understanding Relationships 52

Classifications and Memory 55

The Formation of Higher Taxa 55

Plant Groupings over the Years 60

Literature Cited & Suggested Readings 62



CHAPTER 4

Taxonomic Evidence: Structural and Biochemical Characters 65

Morphology 65

- Duration and Habit 66
- Roots 66
- Stems 67
- Buds 68
- Leaves 68
- Floral Morphology 73

Pollination Biology 79

- Pollination Syndromes 80
- Coevolution between Plant and Pollinator 82
- Deception and Nonnutritive Rewards in
Orchid Pollination 82
- Avoiding Self-Pollination 84

Inflorescences, Fruits, and Seeds 85

- Fruit Types 87
- Seeds 91
- Fruit and Seed Dispersal 91

Anatomy 94

- Secondary Xylem and Phloem 94
- Nodal Anatomy 95
- Leaf Anatomy 96
- Secretory Structures 97
- Crystals 97

- Arrangement of Xylem and Phloem in the Stem 98
- Floral Anatomy and Development 99

Embryology 100

- Ovules and Megagametophytes 101
- Embryo and Endosperm 101
- Agamospermy 102

Chromosomes 103

- Chromosome Number 103
- Chromosome Structure 104
- Methods of Chromosome Study 105

Palynology 108

- Development of the Anther 108
- Pollen Structure, Viability, and
Methods of Study 108

Secondary Metabolites 110

- Alkaloids 110
- Betalains and Anthocyanins 111
- Glucosinolates 111
- Cyanogenic Glycosides 111
- Polyacetylenes 111
- Terpenoids 112
- Flavonoids 113

Proteins 113

Literature Cited & Suggested Readings 114



CHAPTER 5

The Evolution of Plant Diversity 119

Plant Diversity Is the Result of Evolution 120

Variation in Plant Populations and Species 124

- Sources of Variation 124
- Local and Geographic Patterns of Variation 125

Speciation 126

- Reproductive Isolation of Species 128

Origins of Reproductive Isolating Barriers 134

- Hybridization and Introgression 134

- Polyploidy 141
- Plant Breeding Systems 144

Species Concepts 146

- Plant Species Challenges 149

Summary 151

Literature Cited & Suggested Readings 152



CHAPTER 6 An Overview of Green Plant Phylogeny 157

Endosymbiotic Events 159

"Algae" 159

Viridophytes (Green Plants) 160

Chlorophytes 161

Streptophytes 162

Embryophytes (Land Plants) 164

Liverworts 164

Mosses 165

Hornworts 165

Phylogenetic Relationships within Embryophytes 165

Transition to Land 165

Tracheophytes (Vascular Plants) 167

Lycophytes 169

Euphyllophytes 169

Spermatophytes (Seed Plants) 173

Major Characteristics of Spermatophytes 173

Early Evolution of Spermatophytes 175

Extant Lineages of Spermatophytes 176

Angiosperms (Flowering Plants) 180

Flowers and the Angiosperm Life Cycle 180

Time of Origin of Angiosperms 180

Relationships of Angiosperms to Other Groups 181

Relationships within Angiosperms 184

Angiosperm Pollination, Dispersal, and Diversification 186

Summary 187

Literature Cited & Suggested Readings 188



CHAPTER 7 Lycophytes, Ferns, and Gymnosperms 193

LYCOPHYTES 195

Lycopodiales 195

Lycopodiaceae 195 ■ *Selaginellaceae* 197

MONILOPHYTES (FERNS) 198

Equisetales 200

Equisetaceae 200

Psilotales 201

Psilotaceae 201

Ophioglossales 202

Ophioglossaceae 202

LEPTOSPORANGIATE FERNS 202

Osmundales 205

Osmundaceae 205

Salviniales 206

Marsileaceae 206

Cyatheales 207

Cyatheaceae 207

Polypodiales 208

Dennstaedtiaceae 208 ■ *Pteridaceae* 209

Eupolypods I 210

Dryopteridaceae 210 ■ *Polypodiaceae* 210

Eupolypods II 211

Cystopteridaceae 211 ■ *Aspleniaceae* 212

Thelypteridaceae 213 ■ *Woodsiaceae* 213

Athyriaceae 214 ■ *Blechnaceae* 215

Onocleaceae 215

GYMNOSPERMS 216

Cycadales (Cycads) 217

Cycadaceae 217 ■ *Zamiaceae* 218

Ginkgoales 220

Ginkgoaceae 220

Coniferales (Conifers) 222

Pinaceae 223 ■ *Cupressaceae* 225

Podocarpaceae 228 ■ *Araucariaceae* 228

Taxaceae 229

Gnetales 230

Ephedraceae 231

Literature Cited & Suggested Readings 232



CHAPTER 8 Phylogenetic Relationships of Angiosperms 237

ANA GRADE (Amborellales, Nymphaeales, Austrobaileyales) 244

Amborellales 244

Amborellaceae 244

Nymphaeales 245

Nymphaeaceae 246 ■ *Cabombaceae* 248

Austrobaileyales 248

Schisandraceae 248

Mesangiospermae (including Magnoliids, Monocots, Eudicots) 250

Magnoliid Clade (*Magnoliidae*) 250

Magnoliales 250

Magnoliaceae 250 ■ *Annonaceae* 253 ■

Myristicaceae 255

Lurales 255

Lauraceae 255

Canellales 257

Winteraceae 257

Piperales 258

Piperaceae 259 ■ *Aristolochiaceae* 261

A Clade of Uncertain Position 262

Ceratophyllales 262

Ceratophyllaceae 262

MONOCOTS (*Monocotyledoneae*) 263

Alismatales 263

Araceae 263 ■ *Alismataceae* 266 ■

Hydrocharitaceae 268 ■ *Potamogetonaceae* 269

Liliales 269

Liliaceae 271 ■ *Colchicaceae* 272 ■

Smilacaceae 273 ■ *Melanthiaceae* 274

Asparagales 276

Asparagaceae 280 ■ *Ruscaceae* 280 ■

Agavaceae 282 ■ *Hyacinthaceae* 283 ■

Alliaceae 284 ■ *Amaryllidaceae* 285 ■

Asphodelaceae 286 ■ *Iridaceae* 287 ■

Hypoxidaceae 287 ■ *Orchidaceae* 288

Dioscoreales 291

Dioscoreaceae 291

Commelinoid Monocots (*Commelinidae*) 293

Arecales 293

Arecaceae 293

Commelinales 296

Commelinaceae 296 ■ *Haemodoraceae* 298 ■

Pontederiaceae 298

Poales 300

Bromeliaceae 302 ■ *Typhaceae* 305 ■

Eriocaulaceae 307 ■ *Xyridaceae* 307 ■

Juncaceae 309 ■ *Cyperaceae* 309 ■

Restionaceae 311 ■ *Poaceae* 312

Zingiberales 317

Musaceae 317 ■ *Zingiberaceae* 319

Marantaceae 321 ■ *Cannaceae* 323

EUDICOTS (*Tricolpates; Eudicotyledoneae*) 323

Ranunculales 323

Menispermaceae 325 ■ *Ranunculaceae* 327 ■

Berberidaceae 329 ■ *Papaveraceae* 331

Proteales and Other Eudicots 333

Platanaceae 333 ■ *Proteaceae* 334

CORE EUDICOTS (Core Tricolpates) 335

Superrosids (*Superrosidae*) 335

Saxifragales 335

Saxifragaceae 335 ■ *Crassulaceae* 337 ■

Hamamelidaceae 340 ■ *Altingiaceae* 342

Rosid Clade (*Rosidae*) 342

Vitales 343

Vitaceae 343

FABIDS (*Fabidae, Eurosids I*) 343

Zygophyllales 343

Zygophyllaceae 343

Oxalidales 346

Oxalidaceae 346

Celastrales 347

Celastraceae 347

Malpighiales 348

Malpighiaceae 349 ■ *Chrysobalanaceae* 353 ■

Euphorbiaceae 353 ■ *Phyllanthaceae* 356 ■

Clusiaceae 357 ■ *Calophyllaceae* 358 ■

Hypericaceae 359 ■ *Rhizophoraceae* 360 ■

Violaceae 362 ■ *Passifloraceae* 362 ■

Salicaceae 365

Fabales 367

Fabaceae 367 ■ *Polygalaceae* 373

- Rosales 375**
Rosaceae 376 ■ *Rhamnaceae* 385 ■
Ulmaceae 386 ■ *Cannabaceae* 388 ■
Moraceae 389 ■ *Urticaceae* 392
- Cucurbitales 393**
Cucurbitaceae 393 ■ *Begoniaceae* 395
- Fagales 397**
Fagaceae 398 ■ *Betulaceae* 400 ■
Casuarinaceae 403 ■ *Myricaceae* 404 ■
Juglandaceae 404
- MALVIDS (*Malvidae*; *Eurosids II*) 407**
- Geraniales 407**
Geraniaceae 407
- Myrtales 409**
Lythraceae 409 ■ *Onagraceae* 413 ■
Combretaceae 415 ■ *Myrtaceae* 415 ■
Melastomataceae 417
- Brassicales 419**
Brassicaceae 422 ■ *Cleomaceae* 423 ■
Capparaceae 424
- Malvales 424**
Malvaceae 425 ■ *Cistaceae* 429 ■
Dipterocarpaceae 429 ■ *Thymelaeaceae* 430
- Sapindales 430**
Rutaceae 431 ■ *Meliaceae* 435 ■ *Simaroubaceae* 435 ■
Anacardiaceae 437 ■ *Burseraceae* 439 ■
Sapindaceae 439
- SUPERASTERIDS (*Superasteridae*) 442**
- Caryophyllales 442**
Caryophyllaceae 446 ■ *Phytolaccaceae* 448 ■
Nyctaginaceae 449 ■ *Amaranthaceae* 450 ■
Aizoaceae 452 ■ *Montiaceae* 453 ■
Portulacaceae 454 ■ *Cactaceae* 454 ■
Droseraceae 459 ■ *Polygonaceae* 459
- Santalales 461**
Loranthaceae 462 ■ *Viscaceae* 463
- Asterid Clade (*Sympetalae* or *Asteridae*) 465**
- Cornales 465**
Hydrangeaceae 466 ■ *Loasaceae* 467 ■
Cornaceae 468 ■ *Nyssaceae* 470
- Ericales 470**
Balsaminaceae 473 ■ *Polemoniaceae* 473 ■
Fouquieriaceae 476 ■ *Lecythidaceae* 476 ■
Sapotaceae 477 ■ *Ebenaceae* 479 ■
Primulaceae 479 ■ *Theaceae* 481 ■
Ericaceae 482 ■ *Sarraceniaceae* 484
- Core Asterids (*Gentianidae*) 486**
- LAMIIDS (*Lamiidae*; *Euasterids I*) 486**
- Garryales 486**
Garryaceae 486
- Solanales 487**
Solanaceae 487 ■ *Convolvulaceae* 491 ■
Boraginaceae 491
- Gentianales 495**
Rubiaceae 495 ■ *Gentianaceae* 499 ■
Apocynaceae 499
- Lamiales 503**
Oleaceae 504 ■ *Gesneriaceae* 509 ■
Plantaginaceae 510 ■ *Scrophulariaceae* 512 ■
Orobanchaceae 513 ■ *Phrymaceae* 514 ■
Bignoniaceae 515 ■ *Acanthaceae* 517 ■
Lentibulariaceae 519 ■ *Verbenaceae* 519 ■
Lamiaceae 521
- CAMPANULIDS (*Campanulidae*, *Euasterids II*) 523**
- Aquifoliales 523**
Aquifoliaceae 523
- Apiales 525**
Pittosporaceae 525 ■ *Apiaceae* 527 ■ *Araliaceae* 530
- Dipsacales 532**
Caprifoliaceae 532 ■ *Adoxaceae* 534 ■
- Asterales 537**
Campanulaceae 538 ■ *Goodeniaceae* 541 ■
Asteraceae 541
- Literature Cited & Suggested Readings 549**
- APPENDIX ONE**
- Botanical Nomenclature 589**
- Scientific Names 589**
 Phylogenetic Nomenclature—Associating
 Names with Clades Rather than with Ranks 594
 Pronunciation of Scientific Names 595
 Nomenclatural Principles 596
- Requirements for Naming a New Species of
 Vascular Plants 597**
 Hybrid Names 597
 Cultivated Plants 597
- Summary 598**
- Literature Cited & Suggested Readings 598**
- APPENDIX TWO**
- Specimen Preparation and
 Identification 601**
- Collecting Plants 601**
Pressing and Drying Plants 602
**Mounting and Processing Herbarium
 Specimens 604**
Conservation and the Law 604

Plant Identification 605

Keys 605

Floras and Monographs 608

Plant Systematics on the Internet 609

Herbaria, Botanical Gardens, and Taxonomic
Experts 611**Literature Cited & Suggested Readings 612****Glossary 617****Photographic Credits 639****Taxonomic Index 641****Subject Index 669**

Preface

We wrote this book because we believed that there was a need for an explanation of plant systematics (or taxonomy) that can be used in undergraduate courses and that incorporates current exciting developments in the field. In the past two decades abundant new systematic data, especially from DNA sequences, have come forth, and a rigorous phylogenetic approach has established novel ways of analyzing data and practicing systematics.

The three earlier editions of this book have been well received by many students and other botanists. The textbook has been translated into Chinese, French, Italian, Korean, and Portuguese, and the authors of the first edition (Walter S. Judd, Christopher S. Campbell, Elizabeth A. Kellogg, and Peter F. Stevens) received the 1999 Engler Silver Award, an annual award of the International Association of Plant Systematists for the most outstanding book or monograph in plant systematics. Encouraged by this positive reception, we have prepared a fourth edition in order to keep the book as up-to-date as possible.

The basis for this book is the tree of life—the idea that all life is interrelated, like branches on a tree. We deal with the part of this tree occupied by the vascular plants or tracheophytes, and focus on the flowering plants, an important group that dominates most of Earth's terrestrial ecosystems and provides us with medicines, beautiful ornamentals, construction materials, fiber for paper and clothing, and most of our food. Historically, information about these and other attributes of vascular plants was essential to the development of human civilization. Survival rested upon knowing which plants were poisonous or were good to eat; which were potential food for animals; which were good for tools and weapons; which might cure ailments; and which might be useful in many other ways. Systematics as a science grew out of such interests in organisms and evolved from systems of information about the uses of different organisms to a broader understanding of biodiversity. To this end, plant systematists ask questions such as, How should the tremendous diversity of legumes be partitioned or classified into genera and then into species? What are the relationships among the major groups of grasses? How do we know whether or not a plant is a member of the orchid family? This text deals with how these and thousands of similar questions are answered; the final two chapters present some current answers to questions about evolutionary relationships among the major groups of tracheophytes.

Charles Darwin led the way in establishing the evolutionary perspective of modern biology. One impact of this view of life was to make it a major goal of systematics to uncover the evolutionary history—or phylogeny—of groups of organisms. Willi Hennig and W. H. Wagner, along with many others, developed explicit methods of hypothesizing and testing phylogenetic relationships and reflecting these in classifications. We follow a phylogenetic approach throughout this book (as opposed to a phenetic or evolutionary taxonomic/eclectic approach). As far as possible, therefore, we recognize monophyletic and avoid paraphyletic or polyphyletic groups. In the few cases in which a nonmonophyletic family or subfamily has not been divided into monophyletic units, we have placed the taxon name in quotation marks. The monophyly of many genera of angiosperms is questionable, but fewer phylogenetic analyses are available at this level, so generally we have not tried to indicate possible or probable paraphyly or polyphyly of genera.

Chapter 1 introduces and explains the concept of phylogeny, and outlines why systematics is important in biological investigations and to society. Chapter 2 explains how phylogenies are reconstructed from systematic evidence, especially molecular data. The process of transforming evidence into a representation of phylogenetic relationships in an evolutionary tree is first presented using simple hypothetical data and then extended to complex real situations. The chapter examines the construction of phylogenetic trees using Neighbor Joining, Parsimony, Maximum Likelihood, and Bayesian methods. This “primer of phylogeny” also incorporates the conversion of phylogenetic hypotheses into a classification, mapping characters onto trees, and dating phylogenies.

The central position of phylogeny in classification has emerged only recently, but many groups of plants, such as legumes, grasses, mustards, and orchids, have long been recognized. Chapter 3 outlines how systematists perceived groups in the past, how higher taxa were formed, and the historical background of phylogeny. It also provides an explanation of plant groupings over the years. The information on which phylogenies and classifications are based comes from a wide array of sources, including structural aspects of organisms, i.e., morphology, anatomy, cytology, and secondary chemistry (Chapter 4), and DNA features, especially nucleotide sequences (covered in Chapter 2, because of their critical importance in

phylogeny construction). These chapters on phylogeny, classification, and taxonomic evidence provide essential information for understanding the vascular plant groups covered in this book.

Diversification and the evolution of plant species—how plant species form, how they interact, and how we define them, including a presentation of the effects of hybridization—are the fascinating and challenging topics of Chapter 5. Chapter 6 presents an overview of the phylogenetic history of green plants, especially tracheophytes, explains the origin of many of the important features used to identify plants, and lays the foundation for the final two chapters, which focus on vascular plant diversity.

Chapter 7 covers tracheophytes that do not have flowers, including lycophytes, monilophytes, and extant gymnosperms (conifers, cycads, ginkgo, and gnetophytes). Although these plants are certainly important, they are far surpassed in terms of number of species and ecological dominance by the flowering plants or angiosperms, the subject of Chapter 8. Chapters 7 and 8 present the diversity of these groups, with descriptions, illustrations, and discussions of phylogenetic relationships. Exceptionally high-quality illustrations from the Generic Flora of the Southeastern United States, which show taxonomically useful information for many families of plants, and a series of color photographic plates, are special assets of Chapters 7 and 8.

Chapters 7 and 8 also emphasize characterization of major clades of vascular plants, and provide detailed coverage of 187 plant families. Two appendices provide additional information related to plant identification, including botanical nomenclature (the application of scientific names), collection of scientific plant specimens, an overview of plant identification, information about the plant systematics literature, and some useful sites on the Internet.

The science of plant systematics has a large number of specialized terms. We have tried to minimize use of technical language, and to apply those terms used in a consistent and precise manner. The terms used in this book are not only included in the glossary, but they are also boldfaced and defined in the first five chapters and appendices (and included in the Subject Index).

Scientific names (and common names) are included in the Taxonomic Index.

Our knowledge of plant systematics is growing very rapidly, making this an exciting time to study plant sys-

tematics. We encourage students to get caught up in this excitement, to appreciate the beauty and importance of plants, which constitute one of the great branches of the Tree of Life, “which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever-branching and beautiful ramifications” (Charles Darwin, *On the Origin of Species*, 1859, Chap. IV, page 163).

Photo Gallery


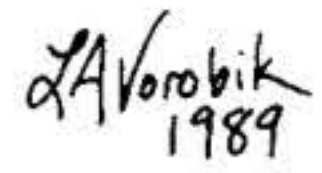


An important tool for plant identification is the website *Photo Gallery of Vascular Plants* that is associated with this book. It contains over 9750 images of flowers, fruits, detailed dissections of flowers and fruits, and other parts of plants. Students can access these images through an alphabetical list of species, an alphabetical list of families (with the species listed alphabetically within each), or a list of orders and families following the arrangement adopted in this text. The *Photo Gallery* is a new feature of the fourth edition, replacing the CD that accompanied earlier editions of this text. This new platform allows for a great expansion in number of images, including those representing diagnostic characters (and variation within) of each of the plant families, floral and fruit dissections, or anatomical structures. An illustrated glossary (a list of defined terms with links to particular images in the *Photo Gallery* illustrating them) is included.

Acknowledgments

This book is a group effort. Although each of us wrote certain chapters, we all benefited from numerous helpful comments from our coauthors. Walter S. Judd had primary responsibility for Chapters 4 and 8, the box covering Hennigian Argumentation in Chapter 2, the two appendices, and the glossary. Christopher S. Campbell was responsible for Chapters 1, 5, and 7; he also contributed the treatment of Rosaceae in Chapter 8, the sections on pollination biology, embryology, chromosomes, and palynology in Chapter 4, and the section on the Internet in Appendix 2. Elizabeth A. Kellogg wrote Chapter 2, a portion of Chapter 1, as well as the treatments for Poaceae, Juncaceae, Cyperaceae, and Santalales in Chapter 8, and the section on arguments against ranks in classifications in Appendix 1. Peter F. Stevens wrote Chapter 3 and Michael J. Donoghue wrote Chapter 6.

The Website *Photo Gallery of Vascular Plants* is the responsibility of Walter S. Judd, Daniel L. Nickrent, Kenneth R. Robertson, J. Richard Abbott, Barbara S. Carlward, Tanja M. Schuster, Christopher S. Campbell, Kurt M. Neubig, Scott Zona, Michael J. Donoghue, and Elizabeth A. Kellogg; this group also provided nearly all of the photographs.

Carroll E. Wood, Jr. and Harvard University generously gave us permission to use numerous plates prepared for the *Generic Flora of the Southeastern United States* and assisted in their organization and electronic digitalization. These beautiful illustrations, which greatly enhance the value of this text, were drawn by a series of exceptionally talented artists:

- | | |
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|  | Wendy B. Zomlefer |

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1

The Science of Plant Systematics



The characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, all true classification being genealogical.

CHARLES DARWIN 1859: 391

What exactly is plant systematics? The question turns out to be more difficult than you may have imagined, because both *plant* and *systematics* are rather hard to define. Considering these concepts in some detail will help us to define the science and clarify our aims.

What Do We Mean by *Plant*?

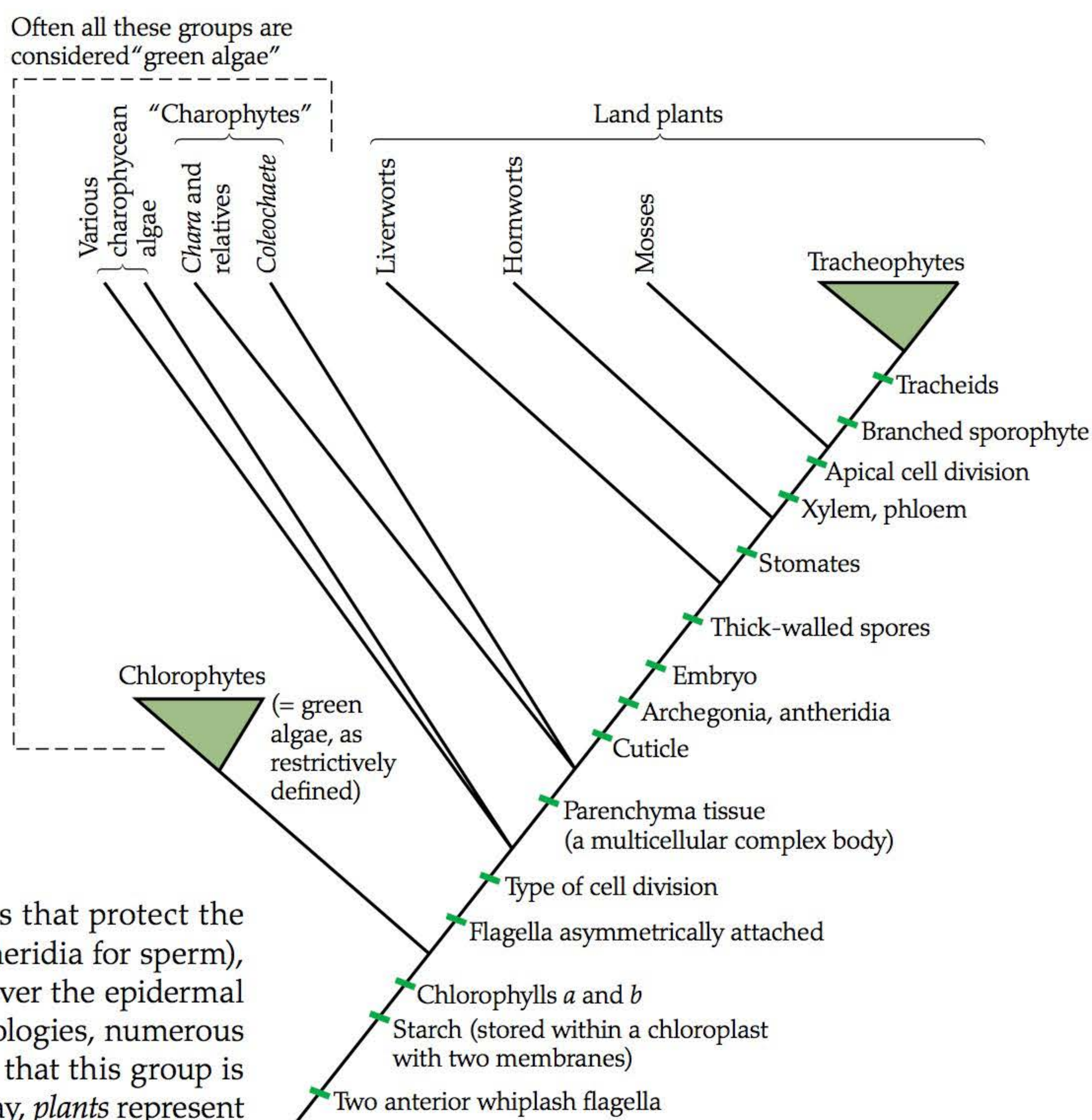
Most people have a commonsense notion of what a plant is: a plant is a living organism that is green and doesn't move around. For some, the notion of a plant encompasses the fungi, which are not green, and botany and plant biology departments in many colleges and universities include mycologists—people who study fungi. For some, the word *plant* is restricted to green organisms living on land and in water. Aquatic photosynthetic organisms, however, encompass a tremendous diversity of life-forms, including “green algae” and non-green algae and related groups.

For the purposes of this book, we will consider the green plants, a major lineage that includes the so-called green algae and the land plants (**Figure 1.1**). Defined in this way, the green plants share a number of features, including (1) the presence of the photosynthetic pigments chlorophylls *a* and *b*; (2) storage of carbohydrates, usually in the form of starch; and (3) the presence of two anterior whiplash flagella at some stage of the life cycle (often modified or sometimes lost).

Within the green plants we will concentrate on the land plants—that is, the **embryophytes** (a few of which actually live in water), whose closest extant relatives are members of the “charophytes,” a green algal group. Land plants have life histories involving alternation of two morphologically distinct bodies (a diploid sporophyte and a haploid gametophyte), thick-walled spores, an embryonic stage



FIGURE 1.1 Phylogeny of green plants (as pictured in a phylogenetic tree). Distinctive structural features that characterize various groups of green plants are indicated on the branches where the characteristics are thought to have evolved. Phylogenetic relationships among the liverworts, hornworts, and mosses are unclear; see also Figure 6.6.



in the life cycle, specialized structures that protect the gametes (archegonia for eggs and antheridia for sperm), and a cuticle (a waxy protective layer over the epidermal cells). Along with these shared morphologies, numerous DNA characters also support the view that this group is *monophyletic*—that is, defined in this way, *plants* represent a single branch on the tree of life.

The land plants consist of three groups of rather small plants—liverworts, hornworts, and mosses—and the **tracheophytes**. *Tracheo* refers to the presence of tracheids—cells specialized for transport of liquids—and the Greek root *phyte* means “plant.” Tracheophytes, sometimes referred to as **vascular plants**, are by far the largest group of green plants, including about 260,000 species. They form the dominant vegetation over much of Earth’s land surface and are the focus of this book.

The great majority of tracheophytes, all but about 13,000 species, are **flowering plants**, or **angiosperms**. In importance to the world’s ecosystems and to human nutrition, medicine, and overall welfare, flowering plants far surpass the other tracheophytes, and most of this book is devoted to the angiosperms.

What Do We Mean by Systematics?

Even though this book focuses primarily on the angiosperm tracheophytes, the basic principles of systematics used here apply to all organisms. **Systematics** is the science of organismal diversity. It entails the discovery, description, and interpretation of biological diversity, as well as the synthesis of information on diversity in the form of predictive classification systems. According to paleontologist George Gaylord Simpson (1961: 7), “Systematics

is the scientific study of the kinds and diversity of organisms and of any and all relationships among them.” This view is so broad that it could encompass what we normally think of as ecology, and perhaps other disciplines as well, so it is necessary to consider in more detail the kinds of relationships that have specifically concerned systematists.

In our view, the fundamental aim of systematics is to discover all the branches of the evolutionary tree of life, to document changes that have occurred during the evolution of these branches, and to the greatest extent possible, to describe all species—the tips of the branches. Systematics is therefore the study of the biological diversity that exists on Earth today and its evolutionary history.

Systematists attempt to reconstruct the entire chronicle of evolutionary events, including the splitting of populations into separate lineages and any and all evolutionary modifications in the characteristics of organisms associated with these branching events, as well as with periods between branching. A secondary but critical aim of systematists is to convey their knowledge of the tree of life—of the terminal branches and their relationships to one another—in an unambiguous system of classification, which can then orient our understanding of life and the world around us. This is the *phylogenetic approach* to systematics.

We explicitly take the view that systematics is not just a descriptive science but that it also aims to discover evolutionary relationships and real evolutionary entities that have resulted from the process of evolution. We take as a starting point the separation of a lineage into two or more lineages. We study the evolutionary modifications that have occurred (and will continue to occur) within these lineages. Our aim is to reconstruct the history of the separation of lineages and the history of their modifications as accurately as possible by bringing as much relevant information as possible to bear on the problem. Systematists continually put forward hypotheses about the existence of branches of the tree of life and test them with evidence derived from a wide variety of sources. Alternative hypotheses are evaluated, and some are provisionally chosen over others.

Some systematists see their work rather differently. They think of themselves as simply describing similarities and differences evident in the organisms around us without reference to any theory. They view branching diagrams such as Figures 1.1 and 1.2 and classifications (see Figure 1.5) only as efficient depictions of these similarities and differences. According to this approach, entities recognized by systematists are summaries of observed information and no more, whereas in our view, these entities are hypothesized branches of the evolutionary tree. Thus our approach extends beyond summation of the data at hand, to statements about entities that we do not directly observe but that we infer came into being through the evolutionary process.

This tension between theory-neutral and theory-grounded approaches pervades the history of science. There have always been those who consider theory-neutral observations to be both possible and desirable and who wish to define the basic terms of scientific discipline in terms of particular operations performed on the data. And there are those, like the authors of this book, whose concepts, definitions, and inferential procedures are explicitly grounded in theory and who wish to go beyond summarizing the evidence at hand to making claims about the world at large.

To some, the distinction we have just made may seem small, and in practice it is true that systematists with different views of their activities all conduct their research in much the same way. We highlight the difference here because it may help interested readers comprehend some of the literature of systematics, and because it helps explain the orientation of our own treatment of plant systematics. Most important, throughout this book we will focus on how we interpret evidence of all kinds in relation to the fundamental aim of systematics stated here. Systematics occupies a central position in evolutionary biology and is playing an increasingly important role in many other disciplines, including ecology, molecular biology, developmental biology, anthropology, and even linguistics and philosophy.

The Phylogenetic Approach

Our view of the science of plant systematics explains an outlook that we hope will emerge again and again throughout this book—namely, that systematics is linked directly and centrally to the study of evolution in general, from the study of fossils to the study of genetic changes in local populations. The basic connection is extraordinarily simple: studies of the process of evolution benefit (usually enormously!) from knowledge of what we deduce has taken place during the evolution of life on Earth. For example, when one sets out a hypothesis about the evolution of a particular characteristic of an organism, it is assumed that the trait of interest did in fact originate within the group being studied. Furthermore, such hypotheses usually rely on some knowledge of the precursor condition from which the trait in question arose.

This kind of information on the sequence of evolutionary events is obtained by systematists who reconstruct the **phylogeny**—the evolutionary history—of a group of organisms. Similarly, studies of the rate of evolutionary change and of the ages and diversification patterns of lineages depend directly on knowledge of phylogenetic relationships.

How Do We Reconstruct Phylogeny?

A phylogeny consists of simple sets of statements of the following nature: groups A and B are more closely related to each other than either is to group C. Consider the simple example of three members of the rose family (Rosaceae): blackberry, cherry, and raspberry (**Figure 1.2**).

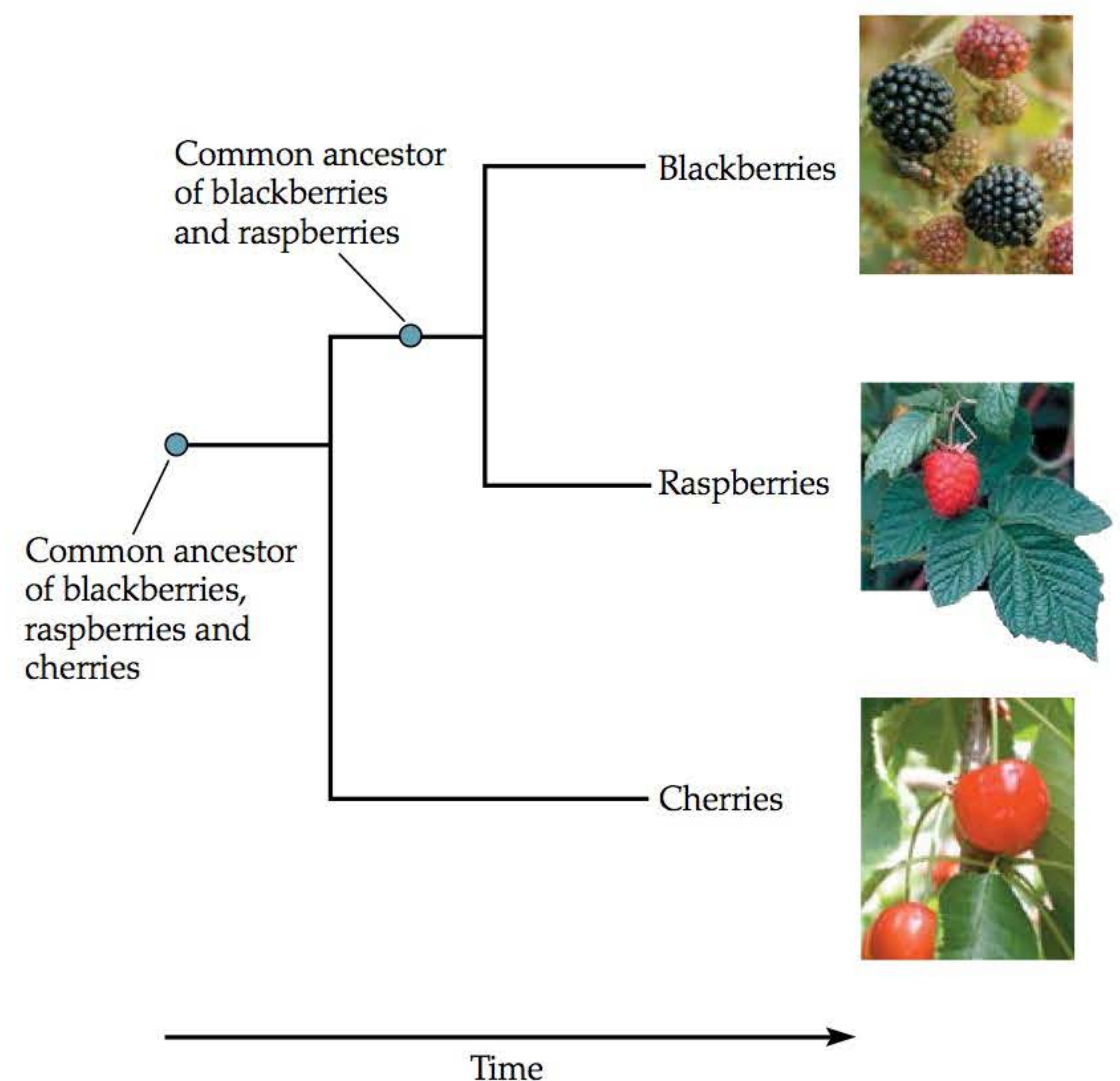


FIGURE 1.2 A simple phylogeny of three groups in the rose family.

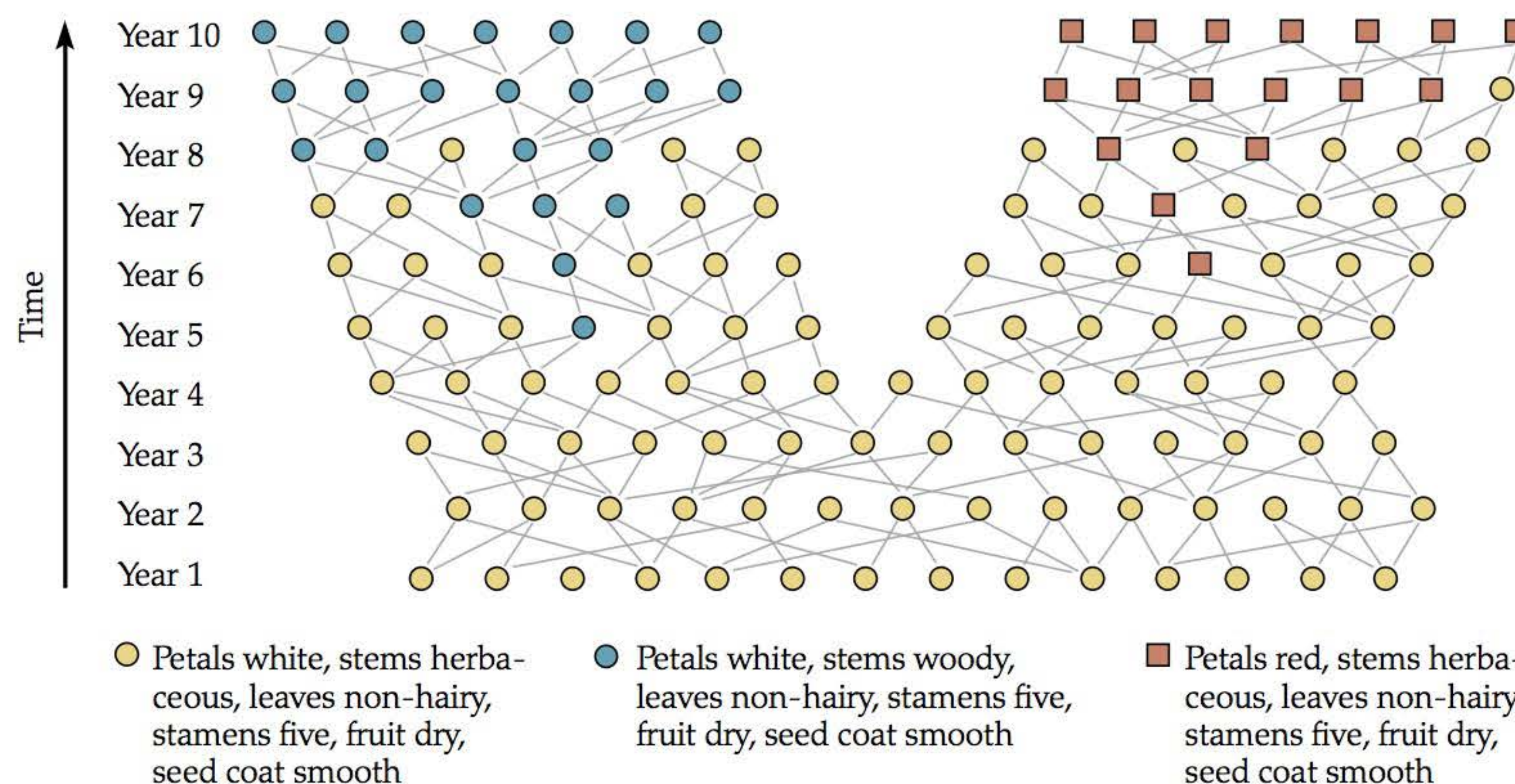


FIGURE 1.3 Evolution of two hypothetical plant lineages. Each circle or square represents an individual plant. Lines extend upward from each plant to its descendants, and downward from each plant to its parents. In year 4, some process divides the population into two populations. A mutation in the population on the left causes a change

Following the injunction “by their fruits ye shall know them,” we can infer evolutionary relationships using only fruits as evidence. Blackberries and raspberries both have numerous small and fleshy fruits (drupes, or stone fruits) that are clustered together (see Chapter 4 for a description of fruit types). Cherry fruits are also drupes, but they are borne singly and are larger than those of blackberries and raspberries.

With this information about the fruits of these three plants, we would judge that blackberries and raspberries are more closely related to each other than either is to cherries. This is equivalent to saying that blackberries and raspberries share a more recent **common ancestor** than either does with cherries. Blackberries and raspberries are said to be **sister groups**, or closest relatives. An abundance of other evidence, from other structural features, chemical constituents, and DNA sequences, leads to the same conclusion about the relationships of these plants. We can present these phylogenetic relationships diagrammatically as an **evolutionary tree** (also known as a **phylogenetic tree** or **cladogram**). This book contains scores of such trees; Figure 1.2 is one of the simplest.

More formally, a phylogenetic tree is a diagram that summarizes the relationships between ancestors and their descendants. Imagine a population of organisms that all look similar to each other. By some process, the population divides into two populations, and these two populations diverge from one another and evolve independently. In other words, two **lineages** (ancestor-descendant sequences of populations) are established. We know this has happened because members of the two new popula-

from herbaceous to woody stems, which is transmitted to descendant plants. Over time, woody-stemmed plants gradually replace all the herbaceous ones in the population. A different mutation in the population on the right leads to a group of plants with red rather than white petals.

tions acquire, by the process of mutation, new characteristics in their genes, and possibly changes in their form, or **morphology**, that make members of one population look more similar to one another than to members of the other population or to the ancestral population. These characteristics are the evidence for evolution.

For example, a set of plants will produce offspring that are genetically related to their parents, as indicated by the lines in **Figure 1.3**. The offspring will produce more offspring, so we can view the population over several generations, with genetic connections indicated by lines.

If for some reason a population divides into two separate populations, each population will have its own set of genetic connections and will eventually acquire distinctive characteristics. For example, in the hypothetical populations shown in Figure 1.3, the population on the right develops red flowers, and the stems of the population on the left become woody. These changes are evidence that each of the populations constitutes a single lineage. The process can be repeated, and each of the new populations can divide again, with each of the newly formed populations acquiring a new set of characteristics. Some of the woody plants now have fleshy fruits, and another group has a spiny seed coat. Meanwhile, some of the red-flowered plants now have only four stamens, and another set of red-flowered plants has hairy leaves (**Figure 1.4**).

The characteristics of plants, such as flower color or stem structure, are generally referred to as **characters**. Each character can have different values, or **character states**. In our example, the character flower color has two states: white and red. The character stem structure also

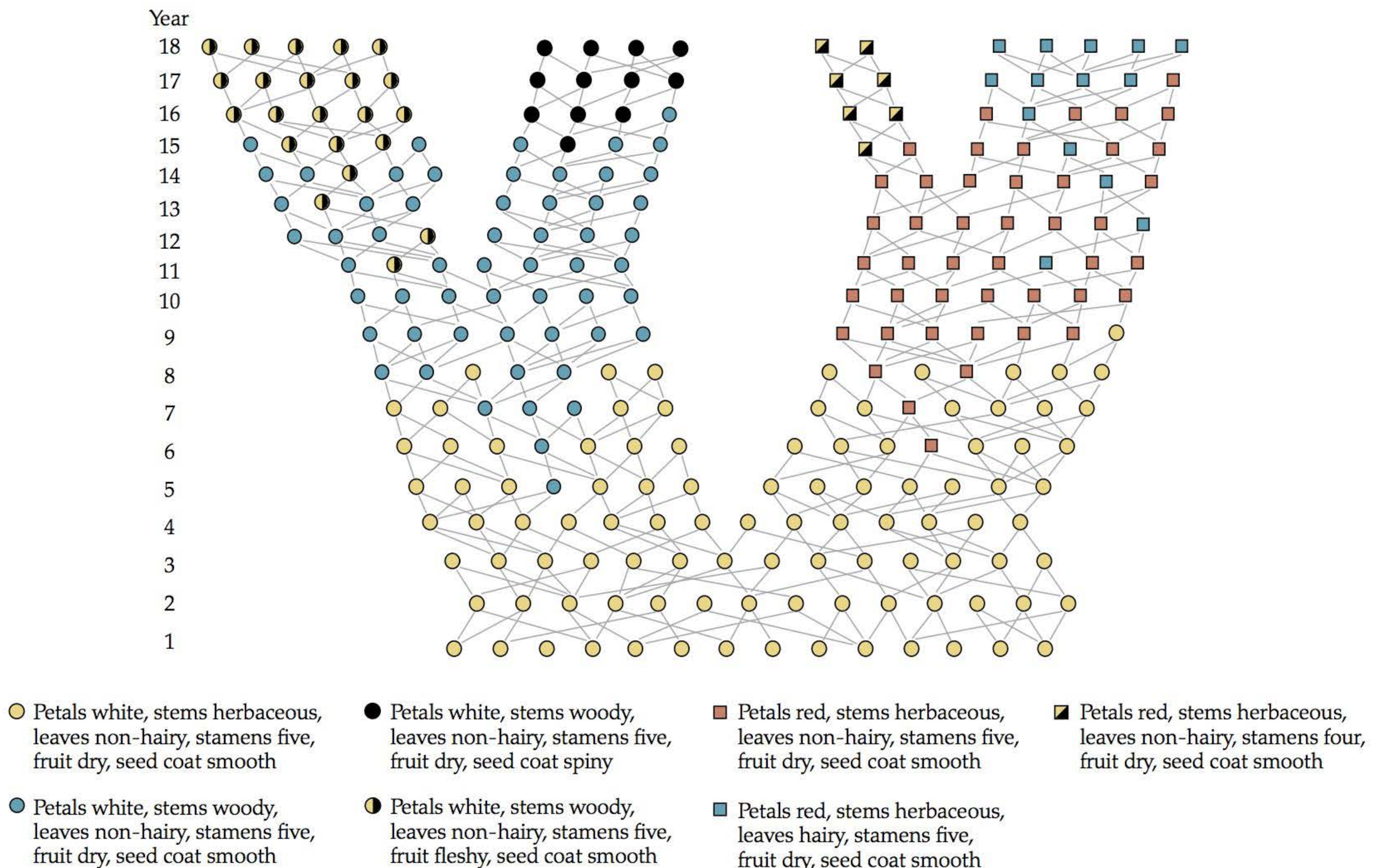


FIGURE 1.4 The same hypothetical set of plants as in Figure 1.3 after 8 more years and two more divisions.

has two states—woody and herbaceous—and so forth. All else being equal, plants with the same character state are more likely to be related to each other than are those with different character states.

The critical point in this example, however, is that character states such as red petals and woody stems are *new*: they are **derived** (or apomorphic) relative to the ancestral population, with its white flowers and herbaceous stems. Only such derived character states tell us that a new lineage has been established; retention of the old character states (white flowers, herbaceous stems, non-hairy leaves, five stamens, dry fruit, smooth seed coat) does not tell us anything about what has happened.

A character state that is derived at one time may become ancestral at a later time. In Figure 1.4, woody stems are derived relative to the original population, but they are ancestral relative to the groups with fleshy fruits or spiny seed coats.

What Is Monophyly?

How does a systematist use a phylogeny to decide which groups of organisms, or **taxa** (singular **taxon**), to name in a classification? A phylogenetic approach demands that each taxon be a **monophyletic** group, defined as a group

composed of an ancestor and all of its descendants (*mono* = single; *phylum* = lineage). The example in Figure 1.2 shows how one identifies monophyletic taxa. Assume for the sake of this example that the rose family contains only these three groups (it is, of course, much larger; see Chapter 8), that all three groups are themselves monophyletic, and that the figure shows the true phylogenetic relationships among the three groups. There are three possible subsets of two of the three taxa: (1) blackberries and raspberries, (2) blackberries and cherries, and (3) cherries and raspberries.

Which subsets of the three groups are monophyletic? Only subset 1 includes all the entities on a single branch of the phylogenetic tree as well as all the descendants of a common ancestor; only subset 1, therefore, is monophyletic. Monophyletic groups are also referred to as **clades**.

Another way to understand monophyly is with the simple rule that a monophyletic group is one that can be removed from the tree by one “cut” of the tree. Try this with Figure 1.2; removal of a nonmonophyletic group, such as blackberries and cherries, requires two cuts. Removal of a nonmonophyletic group from larger phylogenetic trees might require more than two cuts.

This particular definition of monophyly has been adopted only recently (see Chapter 3), and many traditionally recognized plant taxa are not monophyletic by this definition. A familiar example of a commonly recognized

group that is not monophyletic is the “dicots.” These angiosperms have characteristics, such as two cotyledons and flowers with multiples of four or five parts, that make them easily recognized. Nevertheless, they do not form a monophyletic group. The monocots, which apparently are monophyletic, are also descendants of the common ancestor of the “dicots,” and the monocots are nested within the “dicots.” Thus the “dicots” do not contain all the descendants of their common ancestor, and more than one cut is required to remove them from the tree of life.

Chapter 2 discusses monophyly in more detail, as well as how we interpret evidence for or against it. In keeping with our phylogenetic approach, we recognize only monophyletic groups in this book. For example, we reject the nonmonophyletic “dicots” as a formal group, and we place the names of this and other nonmonophyletic groups in quotation marks. A monophyletic group can be recognized as such by its shared derived characters (synapomorphies). **Synapomorphies** are character states that have arisen in the ancestor of the group and are present in all of its members (albeit sometimes in modified form). The concept of synapomorphies was first formalized by Hennig (1966) and Wagner (1980). In recent years, our ability to sequence DNA nucleotides has allowed us to compare the gene sequences of different organisms in our search for synapomorphies. Such studies are the stuff of **molecular systematics**, described in Chapter 2, and their results sometimes overturn long-held views about phylogenetic relationships.

In some cases, the evidence is not unambiguously for or against the monophyly of a group. For example, extant gymnosperms, which include familiar plants such as pines and redwoods, do not form a monophyletic group, according to some data, while other data support their monophyly. Recent molecular data generally support the monophyly of extant gymnosperms, but further studies may well produce evidence to the contrary. We provisionally recognize extant gymnosperms as monophyletic in our classification. Further discussion of this difficult issue can be found in Chapters 6 and 7.

An important exception to the rule of monophyly in the recognition of taxa occurs at the level of species. The problem with monophyly at the species level has to do with the nature of relationships above and below the level of species. Above the level of species, the tree of life generally splits into separate branches, as in Figures 1.1 and 1.2. This is so because blackberries and cherries, for example, do not cross, or hybridize, with one another. Within species, however, branches join through matings between members of a species. Thus, during the separation of one species into two, matings may occur between members of the nascent lineages such that one cannot identify a common ancestor that is unique to either or both species. This problem and others concerning species are taken up in Chapter 5.

The Practice of Plant Systematics

Two important activities of systematists are classification and identification. **Classification** is the placement of an entity in a logically organized scheme of relationships. This scheme is usually hierarchical, consisting of large, inclusive groups of organisms (such as the green plant kingdom, consisting of all green plants) that contain less inclusive, progressively nested groups such as orders, families, genera, and species. The largest, most inclusive groups are the three great **domains** of life: the Bacteria and the Archaea (both of which consist of unicellular, prokaryotic organisms) and the Eukarya (all eukaryotic organisms, both unicellular and multicellular). The domain Eukarya is defined by several synapomorphies, including the presence of a cell nucleus.

Within Eukarya there are many mostly unicellular organisms, commonly lumped together as protists, and the three monophyletic, multicellular kingdoms: the animals, the fungi, and the green plants. Phylogenetic studies deal with groups ranging from domains to species. **Figure 1.5** presents an example of the place of one plant species, *Solidago sempervirens* (seaside goldenrod), in a hierarchical classification scheme (see also Appendix 1). About 1.5 million species of organisms have been described and named, but Earth supports perhaps 10 to 20 times that number of species.

Systematics encompasses the discipline of **taxonomy**. The term *taxonomy* is tied to the word *taxon*. In taxonomy,

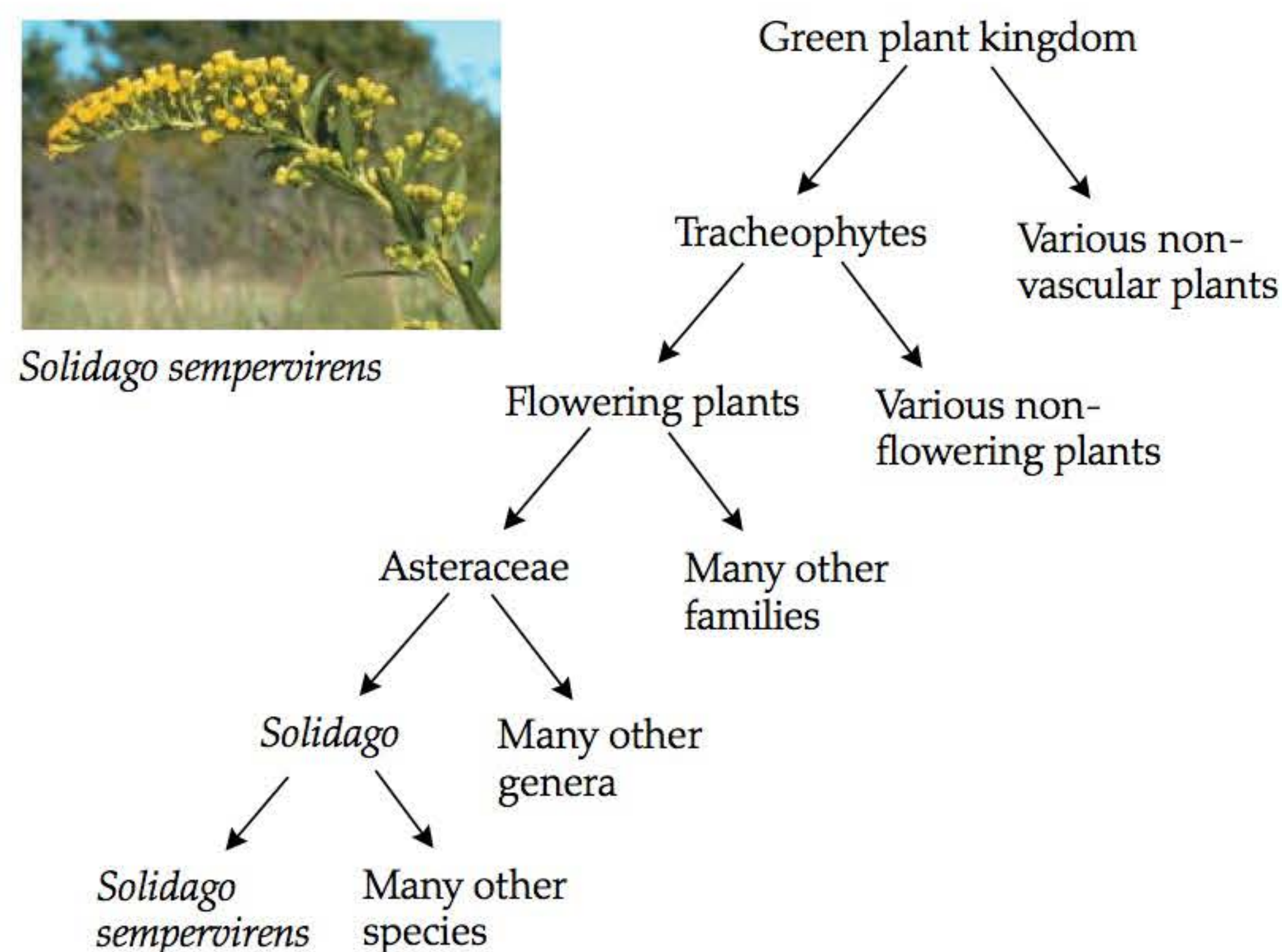


FIGURE 1.5 Portion of a hierarchical classification showing the placement of the species *Solidago sempervirens*, seaside goldenrod. Downward-pointing arrows indicate groups that are nested within the group above. In each case there are two arrows, one leading to the group containing the seaside goldenrod and the other leading to all other groups at the same level in the hierarchy. (Photo by David McIntyre.)

groups of organisms are described and assigned scientific names. Names of taxa give us access to information about them, and thus it is valuable to have one name by which all can refer to a group of plants. This is especially true at the species level, which holds a special place in terms of usefulness and overall importance to humanity. The application of scientific names is the field of **biological nomenclature** (see Appendix 1).

Identification involves determining whether an unknown specimen, such as a plant, belongs to a known, named group. In temperate regions, where the flora is generally well known, one can usually match a plant with a known species. An environmental consultant conducting an inventory of the plants of a temperate-zone salt marsh may find a plant and know it is a goldenrod but be unable to identify the exact species; the numerous species belonging to the goldenrod genus (scientific name *Solidago*) are sometimes difficult to distinguish from one another. The consultant needs to record information about the plant in order to identify it but does not want to damage a plant of an unknown species, because it might be rare or endangered. Therefore, she takes careful notes and photographs to document the plant's appearance. If circumstances render it prudent, it may be helpful to collect a single specimen, which can be preserved by pressing and drying (see Appendix 2) and used to identify a plant accurately.

The fastest way to identify a plant is to consult a professional botanist or well-trained naturalist who is familiar with the plants of a region. Literature can also be consulted: for most temperate regions, there are books devoted to naming and describing the plants; some cover all the plants, while others focus on different portions of the flora.

A third path to identifying a plant is to visit an **herbarium** (plural **herbaria**)—a facility for the storage of scientific plant collections that is a standard component of universities and botanical institutions—and match the information, photographs, and/or specimen with a named specimen there. The Internet, an increasingly useful resource for plant identification, provides images of plants and online keys (Farr 2006; see also Appendix 2).

Plant identification in the tropics is far more challenging than in the temperate zone, not only because tropical floras contain many more species than temperate floras, but also because tropical floras have not been as well studied; vast numbers of tropical species have yet to be recognized, described, named, and collected for herbaria. Here the role of the specialist is critically important, yet there are fewer specialists in this area every year.

Why Is Systematics Important?

Systematics is essential to our understanding of and communication about the natural world. Basic activities of systematics—classification and naming—are ancient human methods of dealing with information about the nat-

ural world, and early in human cultural evolution they led to remarkably sophisticated classifications of important organisms. We depend on many species for food, shelter, fiber for clothing and paper, medicines, tools, dyes, and myriad other uses, and we can know and predict uses for these species in part because of our systematic understanding of the biota.

Although classification has always focused on describing and grouping organisms, it has only relatively recently been concerned with evolutionary phylogenetic relationships. Publication of Charles Darwin's *On the Origin of Species* in 1859 stimulated the incorporation of general evolutionary relationships into classification, an ongoing process that has yet to be fully realized (de Queiroz and Gauthier 1992). A critical step in this process has been the development of a phylogenetic perspective, to which Willi Hennig (a German entomologist, 1913–1976), Walter Zimmermann (a German botanist, 1892–1980), Warren H. Wagner, Jr. (a North American botanist, 1920–2000), and many others have contributed.

The more a classification reflects evolutionary history and phylogeny, the more useful it will be as a predictor. For example, the discovery of biochemical precursors of the drug cortisone in certain species of yams in the genus *Dioscorea* (in the family Dioscoreaceae; see Chapter 8) prompted a search for, and subsequent discovery of, higher concentrations of the drug in other *Dioscorea* species (Jeffrey 1982). The fact that these species are relatives of yams made it likely that they would share genetically controlled features, such as many chemical constituents, with the yams.

Indeed, our knowledge of systematics guides the search for plants of potential commercial importance. In the 1960s, while studying wild plants in the Peruvian Andes, botanist Hugh Iltis collected specimens of a species belonging to the potato genus, *Solanum*, which includes tomatoes. Iltis knew that wild relatives of the cultivated tomato could be important for the breeding of improved tomato crops. He sent some seeds to tomato geneticist Charles Rick in California, who identified the plant as a new species, *Solanum chmielewskii* (named in honor of the late Tadeusz Chmielewski, a Polish tomato geneticist). Rick crossed this wild relative with a cultivated tomato and thus introduced genes that markedly improved the taste of tomatoes (Rick 1982). Similar advances, by the hundreds, have improved yield, disease resistance, and other desirable traits in crops, commercial timber species, and horticultural varieties. Systematics is also critical in biological sciences involving diversity, such as conservation biology, ecology, and ethnobotany.

Systematics advances our knowledge of evolution because it establishes a historical context for understanding a wide variety of biological phenomena, such as ecological diversification and specialization, coevolutionary relationships of hosts and parasites and of plants and pol-

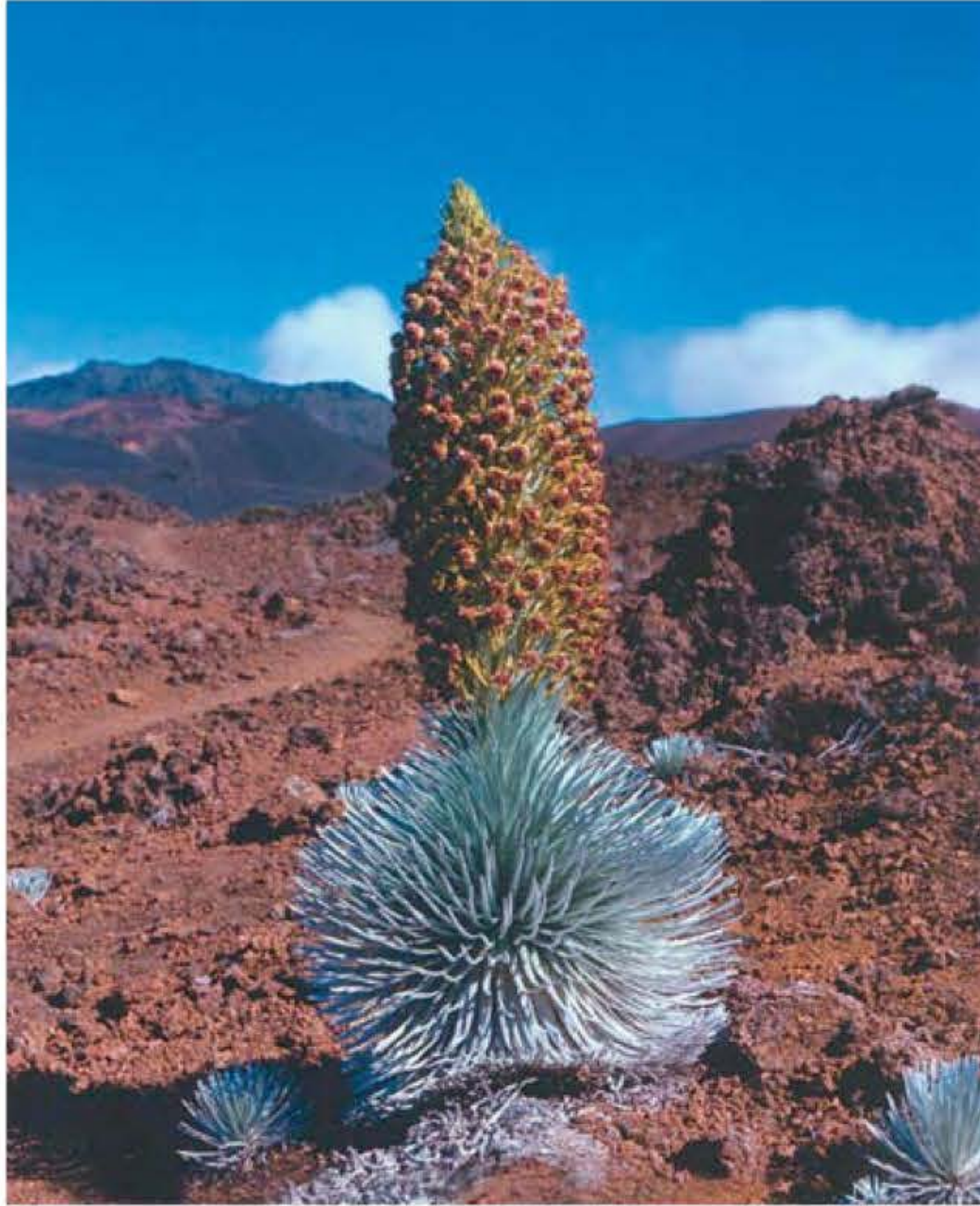


FIGURE 1.6 Habit of one of the Hawaiian silverswords, *Argyroxiphium sandwicense*, showing the basal cluster of sword-shaped leaves and the massive inflorescence, which can be up to 2 meters tall. (Photo courtesy of Sherwin Carlquist and the Botanical Society of America.)

linators, biogeography, adaptation, speciation, and rates of evolution. Three examples will be presented here to show the importance of systematic approaches to evolutionary biology.

The Hawaiian silverswords of the daisy family (Asteraceae) are like many other groups on the Hawaiian Islands in exemplifying evolutionary radiations. The silversword alliance, a monophyletic group of 28 species in three genera (*Argyroxiphium*, *Dubautia*, and *Wilkesia*) that is endemic to the Hawaiian Islands, evolved from a single founding individual of a Californian ancestral species (Baldwin and Robichaux 1995). This group includes some of the most spectacular members of the Hawaiian flora. *Argyroxiphium* species, for example, have a basal rosette of green- or silvery-haired, swordlike leaves from which emerges a terminal inflorescence up to 2 meters tall and with as many as 600 large heads (**Figure 1.6**).

Members of the silversword alliance have diversified into many other growth forms in addition to rosette plants, including trees, shrubs, subshrubs, cushion plants, and lianas. Silverswords occupy an exceptionally wide range of habitats, from 75 to 3750 meters in elevation and from less than 400 to more than 12,300 millimeters in annual precipitation. A common pathway in the evolutionary radiation of the group apparently involves dispersal between islands followed by numerous major ecological shifts along moisture gradients and into bogs.

We can see this pattern of radiation in a phylogeny of the silversword alliance (**Figure 1.7**). When the habitat preferences of silversword species are mapped onto a phylogenetic tree, it is clear that there have been numerous shifts from wet to dry habitats accompanying the evolution of the species. Diversification of the silversword alliance is estimated to have occurred over the past 5.2 million years, which is approximately the age of the oldest high Hawaiian island, Kaua'i. This is a speciation rate of about 0.56 (± 0.17) species per million years (Baldwin 2003), which is remarkably high compared with other groups of plants (see Speciation in Chapter 5).

The second example of systematic approaches' importance concerns evolutionary adaptations for pollination. The genus *Parkia* includes trees of the tropics, especially

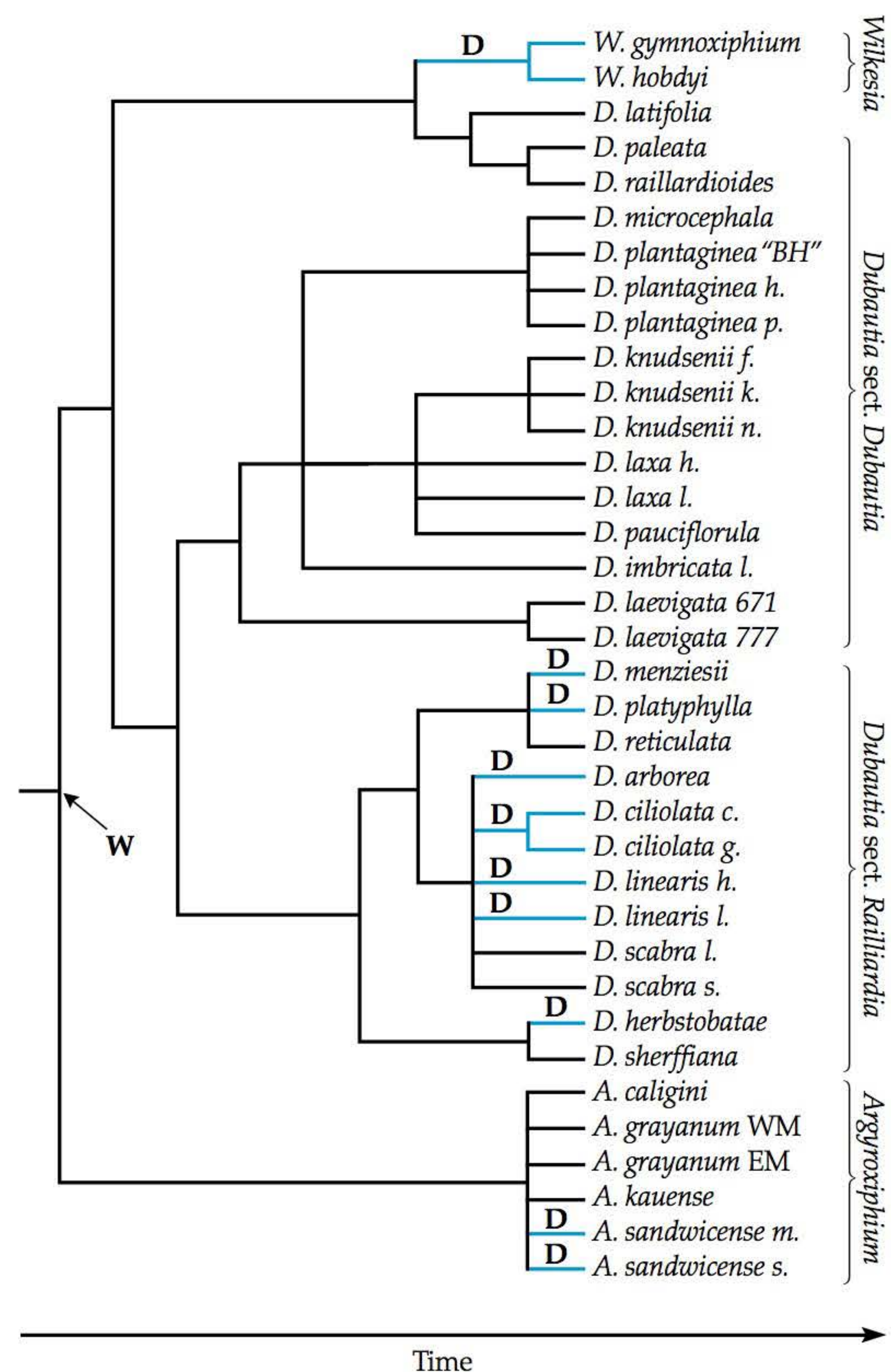


FIGURE 1.7 Phylogenetic tree of the three genera (*Argyroxiphium*, *Dubautia*, and *Wilkesia*) and 25 species of Hawaiian silverswords, based on sequences from internal transcribed spacers in nuclear ribosomal DNA. The letters above the branches of the tree indicate the habitat (D = dry; W = wet) of the lineage defined by the branch. Dry lineages are shown in blue. (After Baldwin and Robichaux 1995.)

rain forests of the Amazon Basin. This genus belongs to the Fabaceae, the legume or bean family (see Chapter 8), and some of its species produce seeds that are a popular vegetable in parts of the tropics. *Parkia* contains a large number of species whose flowers are pollinated by bats. Bat-pollinated *Parkia* flowers open at night, when bats are active, and produce an abundance of nectar that rewards bats for pollinating them. Pollen is brushed onto a bat as it takes nectar from a flower, and the bat completes pollination by depositing pollen onto other flowers it visits.

Until a phylogeny of *Parkia* was established (Luckow and Hopkins 1995), it was not known whether bat pollination had evolved just once or multiple times in *Parkia*. Luckow and Hopkins identified a large clade within *Parkia* in which all the species for which the pollinator was known were bat-pollinated. Bat pollination is not known in *Parkia* outside this clade. This phylogeny was good evidence for a single origin of bat pollination. Several changes in the flowers occurred in the common ancestor of this bat-pollinated clade, the most striking of which was the evolution of specialized flowers that produce a large amount of nectar but no fruit (and which occur on a plant along with functional reproductive flowers). Luckow and Hopkins's phylogeny also suggested that the bat-pollinated species evolved from ancestors that were pollinated by nocturnal bees and thus had flowers that opened at night. Such flowers would have facilitated adaptation for bat pollination. Furthermore, Luckow and Hopkins's phylogeny indicated that the original evolution of bat pollination was followed by continued specialization for bat pollination. For example, the exterior surface of the pollen of some bat-pollinated *Parkia* is sculptured in a special way (Figure 1.8). This kind of pollen surface is called verrucate, which means "wartlike." Members of the Fabaceae that are not closely related to *Parkia* but in which bat pollination has also evolved have similar verrucate pollen. The floral features associated with pollination by vertebrates and other aspects of pollination biology are dealt with in Chapter 4.

Our third systematic approaches example demonstrates the value of phylogeny to **biogeography**, the study of the geographic distributions of organisms. It concerns another group of important tropical trees, the baobabs, some of which are pollinated by bats. There are nine species of baobabs, all in the genus *Adansonia* of the Malvaceae (see Chapter 8). One species is native to Australia, six are confined to Madagascar, and two grow only in Africa. *Adansonia digitata*, the African baobab, is emblematic of sub-Saharan Africa. It can live more than 1000 years and has an unusually massive trunk that can grow as large as 16 meters in diameter. The trunk has the capacity to store large volumes of water, which help the tree survive long periods of drought. The leaves, young sprouts, and seeds are edible and important in the diets of some Africans. The flowers of the African baobab are about 20 centimeters in diameter, open at night, and are pollinated by fruit

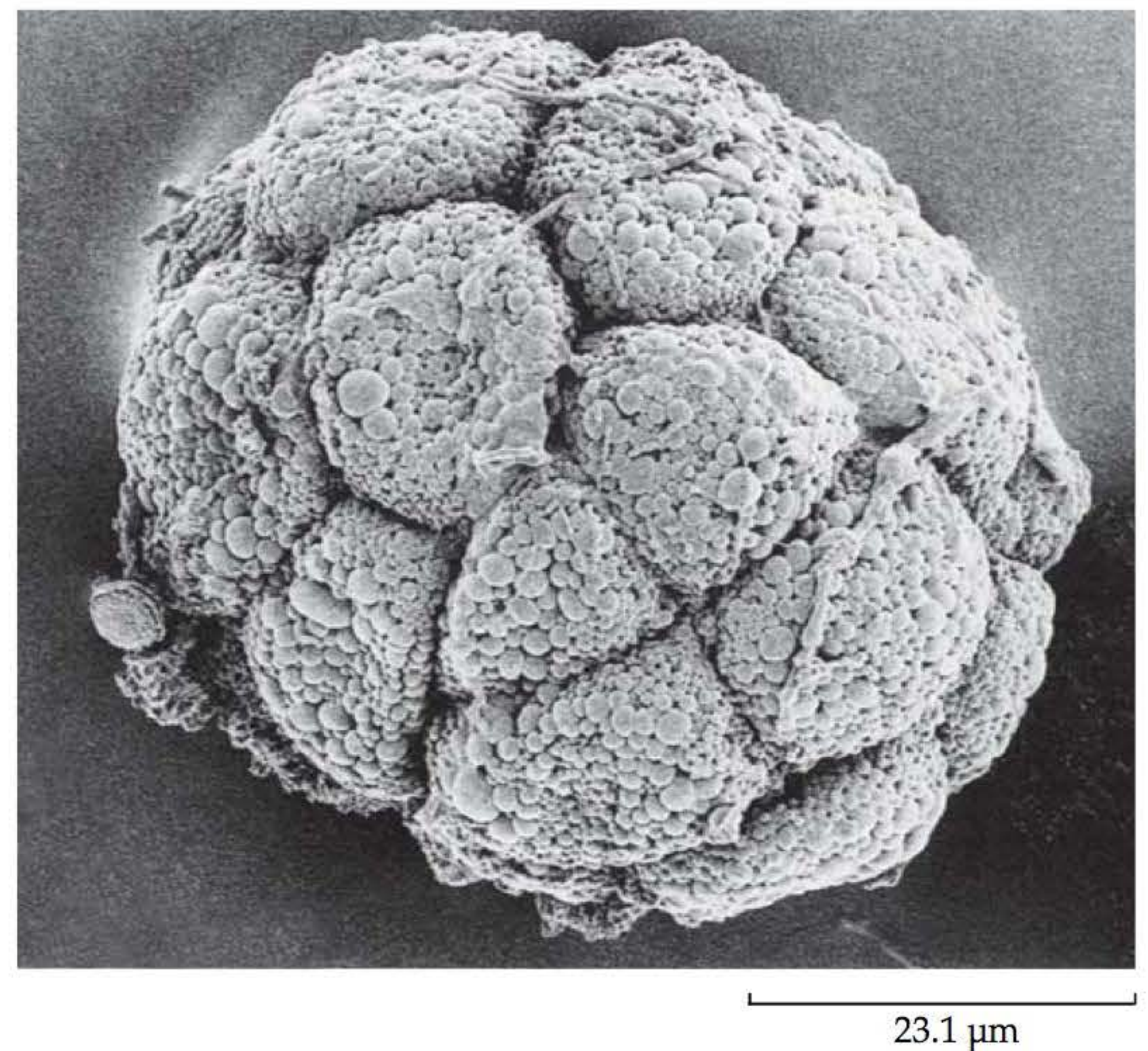


FIGURE 1.8 A cluster of pollen grains of *Parkia sumatrana* var. *streptocarpa*, a bat-pollinated species. The surface of the pollen grains is described as verrucate ("wartlike") and is thought to be a specialization for bat pollination. (From Luckow and Hopkins 1995.)

bats. Bats also pollinate some of the Madagascan baobabs, although a nocturnal lemur also contributes significantly to the pollination of one of these species.

The three landmasses occupied by baobab species were once all part of Gondwana, the former Southern Hemisphere supercontinent that was separated by the forces of plate tectonics and continental drift starting about 120 million years ago. In this case, continental drift resulted in a series of separations, like the splitting of the lineages that make up a phylogeny. It is possible that the nine extant baobab species evolved simply because of the separation of Gondwana. Alternatively, the current geographic distribution of these species could be the result of seed dispersal between the landmasses. We could distinguish between these hypotheses if we had a good fossil record of baobabs, but we do not.

A phylogeny of *Adansonia*, together with estimates of the timing of lineage splitting within the genus, should provide a good test of our two biogeographic hypotheses. Baum et al. (1998) provided such a test with a phylogeny based on nuclear DNA sequences (Figure 1.9). Their phylogeny places the Australian *A. gregorii* as sister to the remainder of the genus. Baum and colleagues then used the rate of evolution of the DNA sequences to estimate the time of divergence of *A. gregorii* from the rest of the genus. If divergence is estimated to have begun before the time when Australia split away from Africa plus Madagascar, then divergence could simply have been the result of the isolation on landmasses separated by continental drift. In-