

# Contents

Sources of DNA Sequence Data	104
Plant Genomes	104
Generating DNA Sequence Data	106
Gene-by-Gene Sequencing	106
Whole-Genome Sequencing	107
Analysis of DNA Sequence Data	107
Mutation Rates	108
Alignment of Sequences	108
Analytic Techniques	108

Preface xiii



## 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



## CHAPTER 2

### Methods and Principles of Biological Systematics 13

How Are Phylogenies Constructed?	13
Determining Evolutionary History	14
Characters, Character States, and Networks	15
Evolutionary Trees and Rooting	16
Choosing Trees	18
Assessing Homoplasy	22
Summarizing Evolutionary Trees	24
The Probability of Evolutionary Change in Characters	25
Do We Believe the Evolutionary Tree?	27

CHAPTER 3	Classification and Phylogeny in Botany
Gene Trees versus Species Trees	109
Classification, Nature, and Stability	110
Molecular Characters	110
Chloroplast Genes and Spacers	112
Mitochondrial Genes	112
Nuclear Genes	113
Restriction Site Analysis	115
Nuclear Genome Mapping	116
Summary	117
Literature Cited and Suggested Readings	118
CHAPTER 4	Botanical Evidence: Cladistic and Biogeographic Characters
Morphology	123
Distribution and Habit	124
Roots	124
Stems	125
Buds	126
Leaves	126
Floral Anatomy	127
Chloroplasts	128
Chromosome Number	129
Chromosomes	129
Methods of Chromosome Analysis	129
Patterns of Variation	130
Development of Taxonomic Methods	130
Pollen	131
Case Studies	131
Guidelines for Recognizing Plant Species	148
Summary	149
Literature Cited and Suggested Readings	151
CHAPTER 5	Comparative Morphology and Systematics
Polination	152
Coevolution	152
Decapitation	152
Case Studies	152
Guidelines for Recognizing Plant Species	148
Summary	149
Literature Cited and Suggested Readings	151
CHAPTER 6	Evolution: Mapping Characters on Trees
Characteristics of Spermatophytes	168
Early Evolution of Spermatophytes	169
Extant Lineages of Spermatophytes	171

### Describing Evolution: Mapping Characters on Trees 29

#### Constructing a Classification 32

Grouping: Named Groups Are Monophyletic	32
Naming: Not All Groups Are Named	33
Ranking: Ranks Are Arbitrary	34

#### Comparing Phylogenetic Classifications with Those Derived Using Other Taxonomic Methods 35

#### Literature Cited and Suggested Readings 37



## CHAPTER 3

# Classification and System in Flowering Plants: Historical Background 39

- Classification, Nature, and Stability 40**
- Understanding Relationships 41**
- Classifications and Memory 45**

**The Formation of Higher Taxa 45**

**Plant Groupings over the Years 50**

**Literature Cited and Suggested Readings 51**



## CHAPTER 4

# Taxonomic Evidence: Structural and Biochemical Characters 53

### **Morphology 53**

Duration and Habit 54

Roots 54

Stems 55

Buds 56

Leaves 56

Floral Morphology 61

### **Pollination Biology 67**

Pollination Syndromes 67

Coevolution between Plant and Pollinator 69

Deception and Nonnutritive Rewards in Orchid  
Pollination 71

Avoiding Self-Pollination 71

### **Inflorescences, Fruits, and Seeds 72**

Fruit Types 75

Seeds 78

Fruit and Seed Dispersal 80

### **Anatomy 81**

Secondary Xylem and Phloem 81

Nodal Anatomy 82

Leaf Anatomy 83

Secretory Structures 84

Crystals 85

Arrangement of Xylem and Phloem in the Stem 86

Floral Anatomy and Development 87

### **Embryology 87**

Ovules and Megagametophytes 88

Agamospermy 89

### **Chromosomes 90**

Chromosome Number 90

Chromosome Structure 92

Methods of Chromosome Study 93

### **Palynology 93**

Development of the Anther 93

Pollen Structure, Viability, and Methods of Study 94

### **Secondary Metabolites 95**

Alkaloids 95

Betalains and Anthocyanins 96

Glucosinolates 97

Cyanogenic Glycosides 97

Polyacetylenes 97

Terpenoids 97

Flavonoids 98

### **Proteins 99**

### **Literature Cited and Suggested Readings 99**



## CHAPTER 5 Molecular Systematics 103

**Sources of DNA Sequence Data 104**

**Plant Genomes 104**

**Generating DNA Sequence Data 106**

Gene-by-Gene Sequencing 106

Whole-Genome Sequencing 107

**Analysis of DNA Sequence Data 107**

Mutation Rates 108

Alignment of Sequences 108

Analytic Techniques 108



## CHAPTER 6 The Evolution of Plant Diversity 119

**Plant Diversity Is the Result of Evolution 120**

**Variation in Plant Populations and Species 123**

Sources of Variation 123

Local and Geographic Patterns of Variation 125

**Speciation 125**

Preservation of Diversity against Gene Flow 127

A Classification of Reproductive Isolating Barriers 128



## CHAPTER 7 An Overview of Green Plant Phylogeny 153

**Endosymbiotic Events 154**

**Miscellaneous "Algae" 155**

**Viridophytes (Green Plants) 156**

Chlorophytes 157

Streptophytes 158

**Embryophytes (Land Plants) 159**

Liverworts 160

Mosses 160

Hornworts 161

**ROSID CLADE 346**

Flowers and the Anolispermum Life Cycle 172

Vitaceae 346

Time of Origin of Anolispermum 172

Relationships of Anolispermum 172

Geraniaceae 808

Relationships Within Anolispermum 172

Gene Trees versus Species Trees 109

**Molecular Characters 110**

Chloroplast Genes and Spacers 112

Mitochondrial Genes 113

Nuclear Genes 113

**Restriction Site Analysis 115**

**Nuclear Genome Mapping 116**

**Summary 117**

**Literature Cited and Suggested Readings 117**

**Origins of Reproductive Isolating Barriers 132**

Hybridization and Introgression 132

Polyplody 140

Plant Breeding Systems 143

**Species Concepts 144**

Case Studies in Plant Species 146

Guidelines for Recognizing Plant Species 148

**Summary 149**

**Literature Cited and Suggested Readings 149**

**Phylogenetic Relationships within Embryophytes 161**

Transition to Land 162

**Tracheophytes (Vascular Plants) 162**

Lycophtyes 165

Euphylllophytes 165

**Spermatophytes (Seed Plants) 168**

Major Characteristics of Spermatophytes 168

Early Evolution of Spermatophytes 169

Extant Lineages of Spermatophytes 171

## **Angiosperms (Flowering Plants) 173**

Flowers and the Angiosperm Life Cycle 175

Time of Origin of Angiosperms 175

Relationships of Angiosperms to Other Groups 176

Relationships within Angiosperms 178



# **CHAPTER 8 Lycophytes, ferns, and Gymnosperms 185**

## **LYCOPHYTES 187**

Lycopodiales 188

*Lycopodiaceae* 188 • *Selaginellaceae* 189

## **MONILOPHYTES (FERNS) 190**

Psilotales 191

*Psilotaceae* 191

Ophioglossales 193

*Ophioglossaceae* 193

Equisetales 193

*Equisetaceae* 193

## **Leptosporangiate Ferns 194**

Osmundales 197

*Osmundaceae* 197

Salviniales 198

*Marsileaceae* 198

Cyatheales 199

*Cyatheaceae* 199



# **CHAPTER 9 Phylogenetic Relationships of Angiosperms 225**

## **ANITA GRADE 232**

Amborellales 232

*Amborellaceae* 232

Nymphaeales 233

*Nymphaeaceae* 233

Austrobaileyales 235

*Illiciaceae* 235

## **Angiosperm Pollination, Dispersal, and Growth Habits 180**

## **Summary 181**

## **Literature Cited and Suggested Readings 181**

## **Polypodiales 199**

*Dennstaedtiaceae* 200 • *Pteridaceae* 201

*Aspleniaceae* 201 • *Thelypteridaceae* 202

  "Woodsiaceae" 203 • *Blechnaceae* 203

*Onocleaceae* 204 • *Dryopteridaceae* 204

*Polypodiaceae* 205

## **GYMNOSPERMS 206**

### **Cycadales (Cycads) 206**

*Cycadaceae* 207 • *Zamiaceae* 208

### **Ginkgoales 208**

*Ginkgoaceae* 208

### **Coniferales (Conifers) 210**

*Pinaceae* 211 • *Cupressaceae* 215 • *Podocarpaceae* 217

*Araucariaceae* 218 • *Taxaceae* 219

### **Gnetales 220**

*Ephedraceae* 221

## **Literature Cited and Suggested Readings 221**

## **MAGNOLIID CLADE 236**

### **Magnoliiales 236**

*Magnoliaceae* 237 • *Annonaceae* 240

*Myristicaceae* 240

### **Laurales 242**

*Lauraceae* 242

### **Canellales 244**

*Winteraceae* 244

### **Piperales 245**

*Piperaceae* 245 • *Aristolochiaceae* 247

<b>A CLADE OF UNCERTAIN POSITION</b>	<b>248</b>		
Ceratophyllales	248		
Ceratophyllaceae	248		
<b>MONOCOTS</b>	<b>249</b>		
Alismatales	249		
Araceae	250 • Alismataceae	252	
Hydrocharitaceae	254 • Potamogetonaceae	256	
Liliales	256		
Liliaceae	257 • Colchicaceae	258 • Smilacaceae	259
Melanthiaceae	260		
Asparagales	262		
Asparagaceae	266 • Ruscaceae	266 • Agavaceae	268
Hyacinthaceae	269 • Alliaceae	270	
Amaryllidaceae	270 • Asphodelaceae	272	
Iridaceae	272 • Orchidaceae	273	
Dioscoreales	275		
Dioscoreaceae	275		
<b>Commelinoid Monocots</b>	<b>276</b>		
Arecales	278		
Arecaceae	278		
Commelinales	280		
Commelinaceae	281 • Haemodoraceae	282	
Pontederiaceae	283		
Poales	285		
Bromeliaceae	287 • Typhaceae	290 • Eriocaulaceae	290
Xyridaceae	292 • Juncaceae	292 • Cyperaceae	294
Restionaceae	296 • Poaceae	296	
Zingiberales	301		
Zingiberaceae	302 • Marantaceae	304	
Cannaceae	306		
<b>EUDICOTS (TRICOLPATES)</b>	<b>307</b>		
Ranunculales	307		
Menispermaceae	308 • Ranunculaceae	309	
Berberidaceae	312 • Papaveraceae	314	
Proteales and Other Tricolpates	316		
Platanaceae	316 • Proteaceae	317	
<b>Core Eudicots</b>	<b>318</b>		
Caryophyllales	318		
Caryophyllaceae	320 • Phytolaccaceae	323	
Nyctaginaceae	324 • Amaranthaceae	324	
Aizoaceae	327 • "Portulacaceae"	328	
Cactaceae	330 • Droseraceae	332 • Polygonaceae	334
Santalales	334		
Loranthaceae	336 • Santalaceae	338	
Saxifragales	338		
Saxifragaceae	338 • Crassulaceae	342	
Hamamelidaceae	342 • Altingiaceae	344	

<b>ROSID CLADE</b>	<b>346</b>		
Vitales	346		
Vitaceae	346		
Geriales	348		
Geraniaceae	348		
Fabids (Eurosids I)	350		
Zygophyllales	350		
Zygophyllaceae	350		
Oxalidales	351		
Oxalidaceae	351		
Celastrales	351		
Celastraceae	351		
Malpighiales	353		
Malpighiaceae	353 • Euphorbiaceae	355	
Phyllanthaceae	359 • Clusiaceae	362	
Hypericaceae	362 • Rhizophoraceae	364	
Violaceae	364 • Passifloraceae	367 • Salicaceae	367
Fabales	371		
Fabaceae	371 • Polygalaceae	377	
Rosales	377		
Rosaceae	379 • Rhamnaceae	388 • Ulmaceae	389
Cannabaceae	391 • Moraceae	392 • Urticaceae	393
Cucurbitales	396		
Cucurbitaceae	396 • Begoniaceae	398	
Fagales	400		
Fagaceae	401 • Betulaceae	404 • Casuarinaceae	406
Myricaceae	406 • Juglandaceae	408	
Myrtales: Incertae Sedis within the Rosids	410		
Lythraceae	412 • Onagraceae	414 • Combretaceae	416
Myrtaceae	416 • Melastomataceae	418	
<b>Malvids (Eurosids II)</b>	<b>420</b>		
Brassicales	420		
Brassicaceae	420		
Malvales	423		
Malvaceae	424 • Cistaceae	427 • Dipterocarpaceae	429
Sapindales	429		
Rutaceae	429 • Meliaceae	432 • Simaroubaceae	435
Anacardiaceae	435 • Burseraceae	437	
Sapindaceae	438		
<b>ASTERID CLADE (SYMPETALAE)</b>	<b>441</b>		
Cornales	441		
Hydrangeaceae	441 • Loasaceae	443 • Cornaceae	443
Ericales	445		
Sapotaceae	445 • Ebenaceae	449 • Primulaceae	450
Theaceae	452 • Ericaceae	452 • Sarraceniaceae	455
Lecythidaceae	455 • Polemoniaceae	457	
<b>Core Asterids</b>	<b>458</b>		

<b>Lamiids (Eusterids I)</b>	<b>459</b>		
Solanales	459		
Solanaceae	459 • Convolvulaceae	462	
Boraginaceae	462		
Gentianales	466		
Rubiaceae	469 • Gentianaceae	471 • Apocynaceae	471
Lamiales	475		
Oleaceae	477 • Gesneriaceae	481	
Plantaginaceae	481 • Scrophulariaceae	484	
Orobanchaceae	484 • Bignoniaceae	486	
Acanthaceae	486 • Lentibulariaceae	488	
Verbenaceae	490 • Lamiaceae	492	

<b>Campanulids (Eusterids II)</b>	<b>494</b>	
Aquifoliales	494	
Aquifoliaceae	494	
Apiales	494	
Apiaceae	495 • Araliaceae	499
Dipsacales	501	
Caprifoliaceae	501 • Adoxaceae	504
Asterales	506	
Campanulaceae	508 • Asteraceae	508

## Literature Cited and Suggested Readings 516

# APPENDIX ONE: Botanical Nomenclature 543

## Scientific Names 543

Arguments against the Use of Ranks in Classification	
548	
Pronunciation of Scientific Names	549
Nomenclatural Principles	549

## Requirements for Naming a New Species 551

Hybrid Names	550
Cultivated Plants	550

## Summary 551

## Literature Cited and Suggested Readings 551

# APPENDIX TWO: Specimen Preparation and Identification 553

## Collecting Plants 553

## Pressing and Drying Plants 554

## Mounting and Processing Herbarium Specimens 556

## Conservation and the Law 556

## Plant Identification 557

Keys	557
Floras and Monographs	558
Plant Systematics on the World Wide Web	560
Herbaria, Botanical Gardens, and Taxonomic Experts	563

## Literature Cited and Suggested Readings 563

## Glossary 567

## Photographic Credits 585

## Taxonomic Index 587

## Subject Index 605

<b>MAGNOLIID CLADE</b>		
Magnoliaceae	352 • Piperaceae	358
Magnoliaceae	352 • Piperaceae	358
Myristicaceae	240	
Laurales	242	
Lauraceae	242	
Canellales	242	
Winteraceae	244	
Piperales	245	
Piperaceae	245 • Aristolochiaceae	247