

PLANT SYSTEMATICS



ELSEVIER *science &
technology books*

• • *Companion Web Site:*

<http://www.elsevierdirect.com/companions/9780123743800>

Plant Systematics, Second Edition, by Michael G. Simpson

Resources for Professors:

- **Figures and appendix material from the textbook**
- **Answers to the end-of-chapter questions**
- **Web link to the author's Plant Systematics Resource website, which includes supplemental teaching material and relevant web links**

Instructor Resources site can be found at <http://textbooks.elsevier.com/web/Login.aspx>, and it is password protected. Please contact your sales representative at textbooks@elsevier.com for access to the Instructor Resources site.



TOOLS FOR ALL YOUR TEACHING NEEDS
textbooks.elsevier.com



**ACADEMIC
PRESS**

To adopt this book for course use, visit <http://textbooks.elsevier.com>.

PLANT SYSTEMATICS

Second Edition

Michael G. Simpson



AMSTERDAM • BOSTON • HEIDELBERG • LONDON
NEW YORK • OXFORD • PARIS • SAN DIEGO
SAN FRANCISCO • SINGAPORE • SYDNEY • TOKYO

Academic Press is an imprint of Elsevier



Cover Images. Front (from left to right): *Hibiscus rosa-sinensis*, Chinese hibiscus (Malvaceae); *Scoliopus bigelovii*, fetid adderstongue (Liliaceae); *Ginkgo biloba*, maidenhair tree (Ginkgoaceae); *Ephedra aspera*, Mormon-tea (Ephedraceae); *Liriodendron tulipifera*, tulip tree (Magnoliaceae). Back: *Lycopodium clavatum*, running clubmoss (Lycopodiaceae). Spine: *Calochortus tiburonensis*, Tiburon mariposa lily (Liliaceae).

Academic Press is an imprint of Elsevier
30 Corporate Drive, Suite 400, Burlington, MA 01803, USA
525 B Street, Suite 1900, San Diego, California 92101-4495, USA
The Boulevard, Langford Lane, Kidlington, Oxford, OX5 1GB, UK

© 2010 ELSEVIER INC. All rights reserved.

No part of this publication may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopying, recording, or any information storage and retrieval system, without permission in writing from the publisher. Details on how to seek permission, further information about the Publisher's permissions policies and our arrangements with organizations such as the Copyright Clearance Center and the Copyright Licensing Agency, can be found at our website: www.elsevier.com/permissions.

This book and the individual contributions contained in it are protected under copyright by the Publisher (other than as may be noted herein).

Notices

Knowledge and best practice in this field are constantly changing. As new research and experience broaden our understanding, changes in research methods, professional practices, or medical treatment may become necessary.

Practitioners and researchers must always rely on their own experience and knowledge in evaluating and using any information, methods, compounds, or experiments described herein. In using such information or methods they should be mindful of their own safety and the safety of others, including parties for whom they have a professional responsibility.

To the fullest extent of the law, neither the Publisher nor the authors, contributors, or editors, assume any liability for any injury and/or damage to persons or property as a matter of products liability, negligence or otherwise, or from any use or operation of any methods, products, instructions, or ideas contained in the material herein.

Library of Congress Cataloging-in-Publication Data

Simpson, Michael G. (Michael George), 1953-
Plant systematics / Michael G. Simpson. – 2nd ed.
p. cm.
ISBN 978-0-12-374380-0
1. Plants—Classification. I. Title.
QK95.S566 2010
580.1'2—dc22

2010009204

British Library Cataloguing-in-Publication Data

A catalogue record for this book is available from the British Library.

For all information on all Elsevier Academic Press Publications
visit our Web site at www.elsevierdirect.com

Printed in China

10 11 12 9 8 7 6 5 4 3 2 1

Working together to grow
libraries in developing countries

www.elsevier.com | www.bookaid.org | www.sabre.org

ELSEVIER

BOOK AID
International

Sabre Foundation

The first edition of this book was dedicated to three mentors I have been 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.

I wish to dedicate the second edition of this book to my wonderful family: Anna, Bonnie, Claire, Lee, and Lori.

CONTENTS

PREFACE.....	ix
--------------	----

ACKNOWLEDGMENTS	xi
-----------------------	----

UNIT I SYSTEMATICS

CHAPTER 1 PLANT SYSTEMATICS: AN OVERVIEW.....	3
---	---

CHAPTER 2 PHYLOGENETIC SYSTEMATICS.....	17
---	----

UNIT II EVOLUTION AND DIVERSITY OF PLANTS

CHAPTER 3 EVOLUTION AND DIVERSITY OF GREEN AND LAND PLANTS.....	55
---	----

CHAPTER 4 EVOLUTION AND DIVERSITY OF VASCULAR PLANTS.....	73
---	----

CHAPTER 5 EVOLUTION AND DIVERSITY OF WOODY AND SEED PLANTS	129
--	-----

CHAPTER 6 EVOLUTION OF FLOWERING PLANTS.....	163
--	-----

CHAPTER 7 DIVERSITY AND CLASSIFICATION OF FLOWERING PLANTS: AMBORELLALES, NYMPHAEALES, AUSTROBAILEYALES, MAGNOLIIDS, CERATOPHYLLALES, AND MONOCOTS.....	181
--	-----

CHAPTER 8 DIVERSITY AND CLASSIFICATION OF FLOWERING PLANTS: EUDICOTS.....	275
---	-----

UNIT III SYSTEMATIC EVIDENCE AND DESCRIPTIVE TERMINOLOGY

CHAPTER 9 PLANT MORPHOLOGY.....	451
---------------------------------	-----

CHAPTER 10 PLANT ANATOMY AND PHYSIOLOGY.....	515
--	-----

CHAPTER 11 PLANT EMBRYOLOGY.....	545
----------------------------------	-----

CHAPTER 12 PALYNOLOGY	561
-----------------------------	-----

CHAPTER 13 PLANT REPRODUCTIVE BIOLOGY.....	573
--	-----

CHAPTER 14 PLANT MOLECULAR SYSTEMATICS.....	585
---	-----

UNIT IV RESOURCES IN PLANT SYSTEMATICS

CHAPTER 15	PLANT IDENTIFICATION	605
CHAPTER 16	PLANT NOMENCLATURE	611
CHAPTER 17	PLANT COLLECTING AND DOCUMENTATION	627
CHAPTER 18	HERBARIA AND DATA INFORMATION SYSTEMS	637

UNIT V SPECIES CONCEPTS AND CONSERVATION BIOLOGY

CHAPTER 19	SPECIES AND CONSERVATION IN PLANT SYSTEMATICS	649
APPENDIX 1	PLANT DESCRIPTION	669
APPENDIX 2	BOTANICAL ILLUSTRATIONS.....	675
APPENDIX 3	SCIENTIFIC JOURNALS IN PLANT SYSTEMATICS.....	679
APPENDIX 4	STATISTICS AND MORPHOMETRICS IN PLANT SYSTEMATICS.....	681
GLOSSARY OF TERMS.....		691
INDEX.....		725

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 courses in plant morphology, diversity, or general botany.

Each chapter has an expanded Table of Contents on the first page, a feature 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). Web sites are listed for some chapters.

The book is classified into units, which consist of one or more chapters. 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. 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, including parsimony, Bayesian, and maximum likelihood methods.

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 its possible adaptive significance. 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 functional significance is pondered. The second section of Chapters 3–5 presents a survey of the diversity of the group in question. New to this second edition are detailed family descriptions of lycophytes (all 3 families treated), ferns (15 of 37 families treated), and gymnosperms (9 of 13 families treated). Family etymologies are included, these, of course, based upon the type genus name; rare conditions and synonyms are enclosed by square brackets. 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 synopsis of their origin. Chapters 7 and 8 describe specific groups of flowering plants. In Chapter 7 the non-eudicot groups are treated, including the earliest diverging angiosperm lineages and the monocotyledons. Chapter 8 covers the eudicots, which make up the great majority of angiosperms. In these two chapters numerous flowering plant families (129 of ca. 400 recognized) are described in detail, accompanied by photographs and illustrations; these are mostly families that are commonly encountered or for which material is usually available to the beginning student. Additional families are not described, but are illustrated with one or more exemplars. I have tried to emphasize diagnostic features a student might use to recognize a plant family, and

have included some economically important uses of family members. 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. The Angiosperm Phylogeny Group III 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, emphasizing the role of computerized database systems in plant collections for analyzing and synthesizing morphological, ecological, and biogeographic data.

Unit 5, Species Concepts and Conservation Biology, new to this second edition, contains a chapter (Chapter 19) that reviews basic plant reproduction and the criteria and concepts of species and infraspecies definitions. In addition, a section on conservation biology reviews the basic concepts of this

field, how it relates to taxonomy and systematics, and its importance to biologists and society.

Lastly, four 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 (available on the Plant Systematics Resources web site). 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. Appendix 4, new to the second edition, gives a brief overview of statistical and morphometric methods and how those may be applied in addressing questions in taxonomy and phylogenetic systematics. The Glossary defines all terms used in the book and indicates synonyms, adjectival forms, plurals, abbreviations, and terms to compare.

Three web sites will be available to be used in conjunction with the textbook: (1) a Plant Systematics Resources site (<http://www.sci.sdsu.edu/plants/plantsystematics>), with web links and materials that are universally available; (2) a companion website (<http://www.elsevierdirect.com/companions/9780123743800>) that includes the chapter figures, appendix material from the textbook, and links to the author's website; and (3) an Instructor Resources site (<http://textbooks.elsevier.com/web/Login.aspx>), 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, What-How-Why, in organizing and clarifying chapter topics: (1) What is it? What is the topic, the basic definition? (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 a 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.

ACKNOWLEDGMENTS

I sincerely thank Andy Bohonak, Bruce Baldwin, Lisa Campbell, Travis Columbus, Gary Emberger, Matt Guilliams, Robert Hattaway, Bruce Kirchoff, Eric Knox, Lucinda McDade, Steve O’Kane, Kathleen Pryer (and her lab group), Jon Rebman, P. van Rijckevorsel, Paula Rudall, Dennis Stevenson, Livia Wanntorp, Annette Winner, and several anonymous reviewers for their comments on various chapters or appendices of the first and second editions of this book. I thank Anna C. Simpson and Lee M. Simpson for technical help. I am grateful to Peter Stevens for up-to-date information on higher level classification of angiosperms from his excellent *Angiosperm Phylogeny Website*. As always, all of these bear no responsibility for any mistakes, omissions, incongruities, misinterpretations, or general stupidities.

Almost all of the illustrations and photographs are the product of the author. I thank the following for additions to these (in order of appearance in text):

The “tree” of Unit 1 opening page (at left) is from Augier, A. 1801. *Essai d’une nouvelle classification des végétaux*. Lyon, Bruyset Ainé. (See Stevens, P. F. 1983. *Taxon* 32: 203–211.) The cladogram (at right) was contributed by Kristen Hasenstab.

The Jepson Herbarium (University of California Press) gave special permission to reproduce the key to the Crassulaceae (Reid Moran, author) in Figure 1.7.

Rick Bizzoco contributed the images of *Chlamydomonas reinhardtii* in Figures 3.2C and 3.3A.

Linda Graham contributed the image of *Coleochaete* in Figure 3.5B.

Figure 4.12A was reproduced from Kidston, R. and W. H. Lang. 1921. *Transactions of the Royal Society of Edinburgh* 52(4): 831–902.

Figure 4.20C was redrawn from Wakasugi, T., M. Sugita, T. Tsudzuki, and M. Sugiura. 1998. *Plant Molecular Biology Reporter* 16: 231–241, by permission.

Figure 4.20D was reproduced from Banks et al. 1975. *Palaeontographica Americana* 8: 77–126, with permission from Paleontological Research Institution, Ithaca, New York.

John Braggins contributed the images of Figure 4.26H–J.

Figure 4.31 was redrawn from Smith, G. M. 1955. *Cryptogamic Botany*, McGraw-Hill Book Company, Inc., New York.

Lawrence Jensen contributed the images of Figure 4.34A,B,E, 4.35D–E,H–J, 4.36C–D, and 4.37C–F.

Vera Svobodova contributed the images of 4.35A–C.

Gerald Carr contributed the image of 4.36F.

Figure 5.9 was reproduced and modified from Swamy, B. G. L. 1948. *American Journal of Botany* 35: 77–88, by permission.

Figure 5.13A,B was reproduced from: Beck, C. B. 1962. *American Journal of Botany* 49: 373–382, by permission.

Figure 5.13C was reproduced from Stewart, W. N., and T. Delevoryas. 1956. *Botanical Review* 22: 45–80, by permission.

Figure 5.19 was redrawn from Florin, R. 1951. *Evolution in Cordaites and Conifers*. *Acta Horti Bergiani* 15: 285–388.

John Braggins contributed the images of Figure 5.22D and 5.24D–F,L.

Figure 5.26B was reproduced from Esau, K. 1965. *Plant Anatomy*. J. Wiley and Sons, New York, by permission.

Mark Olson contributed the images of *Welwitschia mirabilis* in Figure 5.27B–E.

Figure 6.5 was based upon Jack, T. 2001. *Trends in Plant Science* 6: 310–316.

Figure 6.18A–C was redrawn from Thomas, H. H. 1925. *Philosophical Transactions of the Royal Society of London* 213: 299–363.

Figure 6.18D–F was redrawn from Gould, R. E. and T. Delevoryas. 1977. *Alcheringa* 1: 387–399, by permission.

Figure 6.19A was contributed by K. Simons and David Dilcher (©); Figure 6.19B was contributed by David Dilcher (©) and Ge Sun.

Stephen McCabe contributed the images of *Amborella* in Figures 7.3A,C.

The Arboretum at the University of California-Santa Cruz contributed the image of *Amborella* in Figure 7.3B.

Sandra Floyd provided the image of *Amborella* in Figure 7.3D.

Jeffrey M. Osborn and Mackenzie L. Taylor contributed the images of the Cabombaceae in Figure 7.5.

Jack Scheper contributed the image of *Illicium floridanum* in Figure 7.6A.

Figure 7.18 was reproduced from Behnke, H.-D. 1972. *Botanical Review* 38: 155–197, by permission.

Constance Gramlich contributed the image of *Amorphophallus* in Figure 7.25C.

Wayne Armstrong contributed the image of a flowering *Wolffia* in Figure 7.25G.

John Kress contributed the Zingiberales drawing in Figure 7.56.

Will Cook contributed the images of *Hamamelis virginiana* in Figure 8.12A–C and of *Ulmus alata* in 8.52G.

Figure 8.18B was reproduced from Behnke, H.-D. 1972. Botanical Review 38: 155–197, by permission.

Gerald Carr contributed the images of *Hillebrandia sandwicensis* in Figure 8.55A,B and of *Juglans hindsii* in Figure 8.60D–H.

The Rampant Gardener contributed the image of *Juglans regia* in Figure 8.60J.

Jerry Green contributed the image of *Crossosoma bigelovii* in Figure 8.61A.

Reid Moran contributed the image of *Crossosoma californicum* in Figure 8.61B–D, of *Koeberlinia spinosa* in Figure 8.70J–L, and of *Eucnide urens* in Figure 8.87B.

Mark Olson contributed the images of *Moringa* spp. in Figure 8.70M–Q.

Serge Aubert (Station Alpine Joseph Fourier) contributed the image of *Loasa tricolor* in Figure 8.87A.

Gerald Carr contributed the images of *Ardisia crenata* in Figure 8.92A,B.

Steven Swartz contributed the images of *Heliamphora* sp. in Figure 8.96F,G.

Matt Guilliams contributed the image of *Pholisma sonorae* in Figure 8.102C.

David G. Smith contributed the images of *Phryma leptotachya* in Figure 8.115I,J.

Michael Silveira contributed the image of *Linnaea borealis* in Figure 8.127C.

Michael Mayer contributed material of *Scabiosa*, photographed in Figure 8.128.

The brass microscope image of the Unit III opening page is courtesy of Allan Wissner (www.antique-microscopes.com).

Figure 9.12 was redrawn from Hickey, L. J. 1973. American Journal of Botany 60: 17–33, by permission.

Darren Burton prepared several illustrations in Chapter 9.

Figure 13.4A was redrawn from Weberling. 1989. Morphology of Flowers and Inflorescences. Cambridge University Press, Cambridge, New York, by permission.

Figure 13.4B was redrawn from Kohn et al. 1996. Evolution 50: 1454–1469, by permission.

Jon Rebman contributed the images in Figure 13.7D,E.

Figure 14.4 was redrawn from Wakasugi, T., M. Sugita, T. Tsudzuki, and M. Sugiura. 1998. Plant Molecular Biology Reporter 16: 231–241, by permission.

The Herbarium at the San Diego Natural History Museum contributed the images in Figure 17.2.

Jon Rebman contributed the image of the herbarium sheet in Figure 18.2.

Figure 19.6 was redrawn from Huang et al. 2005. Journal of Plant Research 118: 1–11, by permission.

Figure 19.9 was redrawn from Baldwin. 2000. Madroño 47: 219–229, by permission.

Dinna Estrella contributed the stippled line drawing in Appendix 2.