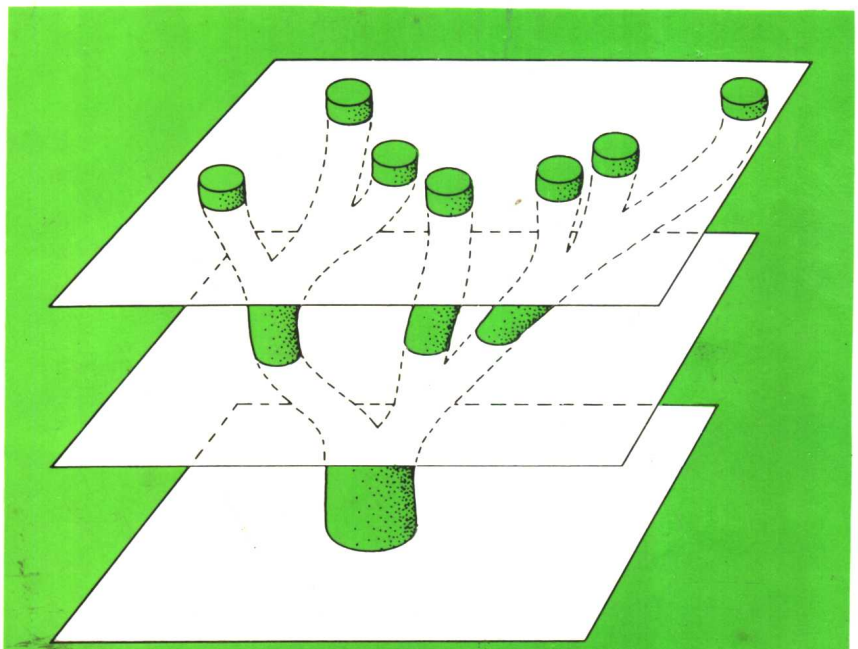
TOD F. STUESSY

PLANT TAXONOMY



THE SYSTEMATIC EVALUATION OF COMPARATIVE DATA

TOD F. STUESSY

Plant Taxonomy

The Systematic Evaluation of Comparative Data

 *Columbia University Press New York*

COLUMBIA UNIVERSITY PRESS
New York Oxford

Library of Congress Cataloging-in-Publication Data

Stuessy, Tod F.
Plant taxonomy : the systematic evaluation of comparative data /
Tod F. Stuessy.
p. cm.
Includes bibliographical references.
ISBN 0-231-06784-4
1. Botany—Classification. I. Title.
QK95.S78 1989
581'.012—dc20 *89-17401*
CIP

Book design by Jennifer Dossin
Casebound editions of Columbia University Press books are Smyth-sewn
and printed on permanent and durable acid-free paper
♾

Printed in the United States of America
c 10 9 8 7 6 5 4 3 2 1

PREFACE

THIS BOOK is designed to introduce the upper-level undergraduate or beginning graduate student to the philosophical and theoretical aspects of plant taxonomy. At the present time there is no text that fills this need. The closest book in depth and breadth of coverage would be the excellent *Principles of Angiosperm Taxonomy* by Davis and Heywood (1963), which is now more than twenty-five years old. In particular, the past decade has seen a proliferation of articles and books on phenetic and cladistic philosophies and methodologies, to the extent that there is now a real need for a balanced account of these new developments for professors and students of plant taxonomy. The literature is extensive, the debates often acrimonious, and the polarization of the broad community of systematic biologists acute. Definitions have been changed, historical perspectives and precedents have been ignored or interpreted differently, and numerous viewpoints have been offered. The challenge is immense to the teacher and student of plant taxonomy to sort this all out and apply these concepts and methods to actual situations. The recent books, *Plant Taxonomy and Biosystematics* (Stace 1980), *Introduction to Principles of Plant Taxonomy* (Sivarajan 1984), and *Fundamentals of Plant Systematics* (Radford 1986) are steps in the proper direction, but they lack the detail of coverage of most topics desirable for advanced students.

The present text is divided into two parts. Part 1 contains the principles of taxonomy including the importance of taxonomy and systematics, characters, different approaches to biological classification, and concepts of categories. These are the basic chapters that tell what taxonomy is and how one goes about doing it. As will be obvious, evolutionary (= phyletic) taxonomy is favored as the best approach to biological classification. Considerable attention has also been given to phenetics and cladistics, however, and a balanced presentation has been attempted despite my own biases. We are now entering a new phase of biological classification in which phyletic classifications can be constructed explicitly, called here "the New Phyletics" (chapter 9), and it is hoped that this book will stimulate more interest in this direction.

Part 2 outlines different types of data used in plant taxonomic studies with suggestions on their efficacy and modes of presentation and evaluation. Not all types of data have been included, but the most commonly used ones are discussed with references given. The equipment and financial resources needed for gathering each type of data also are listed briefly. The main point has been to

show (by illustrations and references) the incredible diversity of data used for taxonomic purposes in angiosperms and to stimulate their further use by students and workers. Specific case studies in which these data are employed are fewer than the displays and discussions of data themselves.

Many quotes are placed throughout the text to emphasize the historical perspective, which is so important in the development of taxonomic terminology and philosophy. Similarly, the life-span for historically important workers is given to help show the total period in which the individual lived and worked. The literature cited is not exhaustive, but it is extensive so that most topics are covered reasonably thoroughly and can serve as a good springboard for additional readings in a particular area. The cutoff date for new literature additions was July 1, 1988.

The view of taxonomy presented here is primarily a personal one. I have tried to determine what I do operationally as a practicing plant taxonomist and to view these activities within a meaningful conceptual framework. These ideas have been augmented and refined by the concepts of others, which have been cited when they could be recalled. Some ideas that seem original to me now were stimulated no doubt many years ago by miscellaneous readings or comments from colleagues or students, the sources of which have long been forgotten. I have placed particularly heavy emphasis on concepts throughout these chapters, because I believe strongly that the most creative taxonomy is done by those who know (or at least strive to know) conceptually what they actually are doing. I hope this perspective will be stimulating and useful.

ACKNOWLEDGMENTS

ALMOST EVERY author owes debts of gratitude to numerous people for having encouraged and helped bring a book to successful completion. This work is no exception. Drs. Patrick Dugan and Emanuel D. Rudolph, former Dean of the College of Biological Sciences and former Chairman of the Department of Botany, respectively, of Ohio State University, courteously arranged a sabbatical leave for me in Fall quarter, 1982, during which time the first full draft of the book was initiated. At this same time, Drs. William Anderson and Edward Voss of the Herbarium, University of Michigan, made generous arrangements for my stay at their institution which allowed me to work uninterruptedly and put the writing of this book on schedule.

Many individuals have read various drafts of the manuscript and made many helpful suggestions. A very early (and very different) draft was read by W. P. Adams, S. B. Jones, Jr., J. E. Rodman, O. T. Solbrig, B. L. Turner, J. Wahlert, and R. L. Wilbur. The complete final draft was read by V. H. Heywood, S. B. Jones, Jr. and B. L. Turner. Chapters of the final manuscript were read by (chapter numbers in parentheses): W. G. Abrahamson (23), R. E. J. Boerner (23), B. A. Bohm (21), P. D. Cantino (8), D. J. Crawford (1-4), T. J. Crovello (4, 7), R. H. Eyde (15, 16), K. Jones (19, 20), L. W. Macior (22), J. W. Nowicke (18), J. M. Herr, Jr. (17), V. Raghavan (16, 17), F. D. Sack (16), J. J. Skvarla (18), R. R. Sokal (7), D. E. Soltis (19), R. W. Spellenberg (8), W. P. Stoutamire (22), and R. L. Wilbur (10–14). E. D. Rudolph provided valuable bibliographical assistance.

Gratitude is expressed to numerous holders of copyrights of figures and tables reproduced in this book who have given permission to use these materials. These include authors, publishers, and editors of societal journals. Obviously in a book such as this, which depends so heavily on illustrations (especially in part 2), these permissions were essential for successful completion of the project. Credits to the authors are given in the legends to the presented material with full references to place of publication in the Literature Cited. The publishers and journals which have given generously their permissions are: Knopf, New York; Academic Press, London; *American Journal of Botany; American Scientist; American Zoologist; Annals of the Missouri Botanical Garden; Annual Review of Ecology and Systematics;* American Elsevier, New York; *Australian Journal of Botany; Bartonia; Biotropica; Botanical Journal of the Linnean Society; Botaniska Notiser;* Cambridge University Press, Cambridge; *Canadian Journal of Botany; Canadian Journal of Genetics and Cytology; Chromosoma* (Berlin); DLG-Verlags-GmbH,

Frankfurt; *Evolution; Evolutionary Biology; Fieldiana, Botany;* Garrard, Champaign, Ill.; George Allen & Unwin, London; *Grana;* Harper & Row, New York; Hodder and Stoughton, London; *Journal of the Arnold Arboretum; Journal of the Elisha Mitchell Scientific Society;* Wiley, New York; *Kew Bulletin; Madroño;* McGraw-Hill, New York; *Memoirs of the New York Botanical Garden; New Phytologist; Nordic Journal of Botany; Ohio Journal of Science; Oikos; Opera Botanica;* Oxford University Press, Oxford; Pergamon Press, Oxford; *Plant Systematics and Evolution;* Prentice-Hall, Englewood Cliffs, New Jersey; *Proceedings of the Academy of Natural Sciences of Philadelphia; Rhodora; Science; Smithsonian Contributions to Botany;* Springer-Verlag, Berlin; *Systematic Botany; Systematic Botany Monographs; Systematic Zoology; Taxon; University of California Publications in Botany;* University Press of Kansas, Lawrence; University Park Press, Baltimore; Freeman, San Francisco; Junk, The Hague; Wadsworth, Belmont, California; and Collins, London. Permission was also granted by the British Museum (Natural History) to reproduce figure 15.1. All new figures were drawn by David Dennis and Lisa Mary Einfalt.

Parts of this book have been published already in modified form. The history of botanical cladistics in chapter 8 appeared with less detail in Duncan and Stuessy (1985), and some of the material on species concepts in chapter 11 is to be published in Stuessy (in press).

The editors of Columbia University Press were extremely helpful for their combination of understanding, patience, and professional assistance. Ed Lugenbeel was more than an editor—he was a friend and counselor too. With his competent help and that of the Productions and Marketing staffs, a much higher level of quality has been achieved in this book than would have been possible solely through my efforts.

Significant persons in this undertaking have been Jonathan Abels and my wife, Patricia, who helped check inconsistencies between text citations and the Literature Cited. Special thanks also go to John W. Frederick for assistance with various aspects of manuscript preparation.

Finally, and of the greatest importance, have been the many students who initially stimulated me to write this book, and who have worked through the several drafts and offered useful criticisms. Particularly helpful have been Wen Jun, Thomas Lammers, and James Zech. Without this constant prodding, I doubtless would never have finished the task.

PLANT TAXONOMY

In these days when Molecular Biology is beginning to be seen as a restricted science, narrowing our vision by concentrating on the basic uniformity of organisms at the macromolecular level, the need for taxonomists to draw attention to the enormous diversity and variation of this earth's biota becomes more and more pressing.

V. H. Heywood (1973a:145)

In other words, the field of taxonomy in a way epitomizes the work of all other branches of biology centered on the organism itself, and brings the varied factual information from them to bear on the problems of interrelationship, classification and evolution. Thus taxonomy, as has been aptly remarked, is at once the alpha and omega of biology.

R. C. Rollins (1957:188)

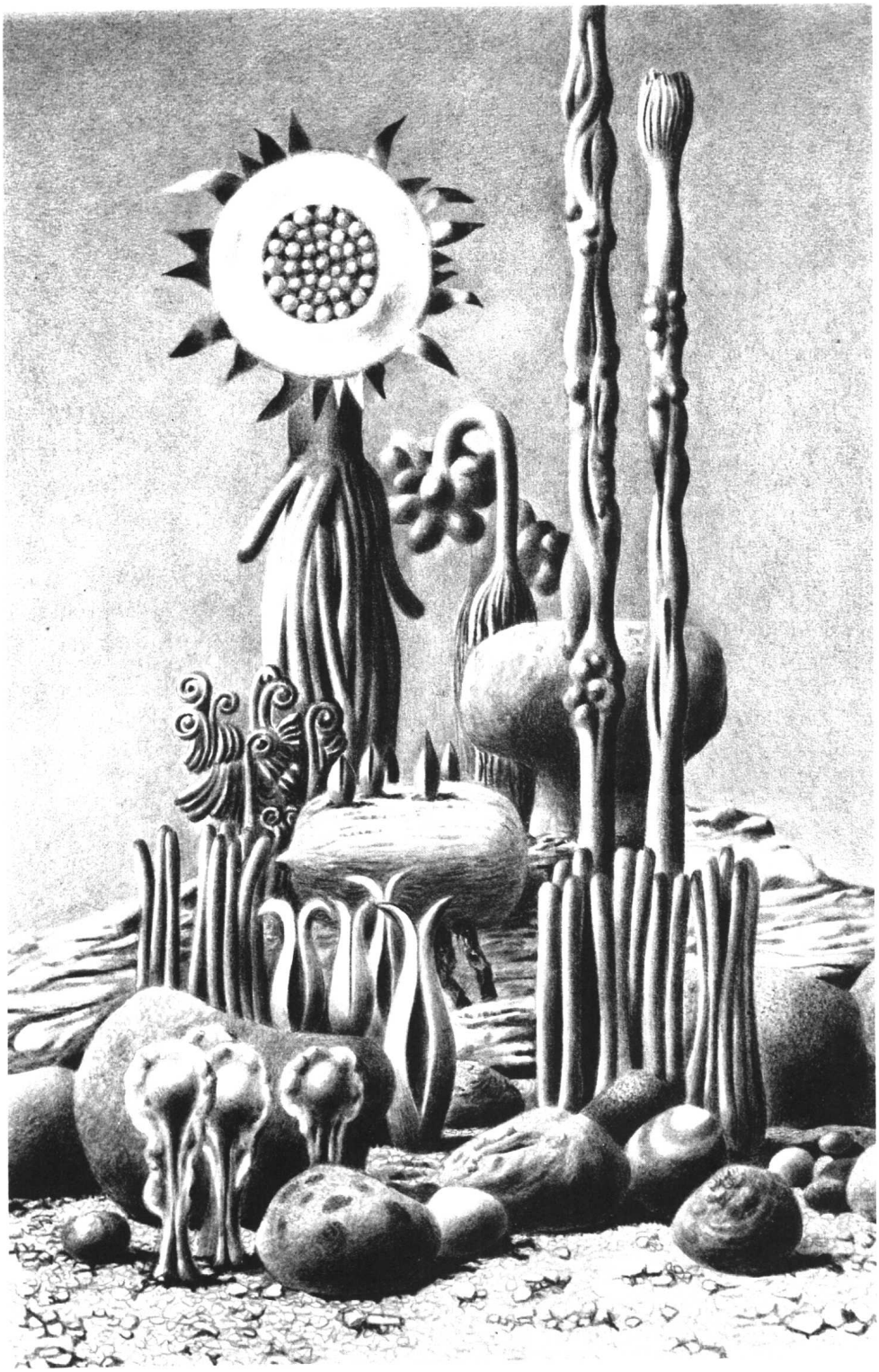
Plant taxonomy has not outlived its usefulness: it is just getting under way on an attractively infinite task.

L. Constance (1957:92)

CONTENTS

PART ONE

Principles of Taxonomy



SECTION ONE

The Meaning of Classification

TAXONOMY IS dynamic, beautiful, frustrating, and challenging all at the same time (fig. 1.1). It is demanding philosophically and technically, yet it offers intellectual rewards to the able scholar and scientist. It can be manifested in works of incredible detail as well as in logical and philosophical conceptualizations about the general order of things. It has strong implications for interpreting the reality of the world as we can ever hope to know it.

Because taxonomy has deep historical roots, the past is never escaped. This places an increasing burden upon practitioners to understand old and new material. The past must be dealt with for older results and every new discovery must be digested and incorporated. As Constance has aptly put it, "My ideal taxonomist, therefore, must be very versatile indeed, and should preferably be something of a two-headed [i.e., two-faced] Janus, so that one set of eyes can look back upon and draw from the experience of the past, and the other pair can be focused upon deriving as much of value as possible from developments on the present scene" (1951:230).

Taxonomy is a synthetic science, drawing upon data from such diverse fields as morphology, anatomy, cytology, genetics, cytogenetics, and chemistry. It has no data of its own. Every new technical development in these other areas of science offers promise for improved portrayal of relationships of organisms. This is a demanding aspect of taxonomy for a practicing worker, because it is virtually impossible to understand completely all of these different data-gathering methods, yet highly desirable to be able to master as many as possible. Furthermore, the accumulation of data and their interpretation never cease. Not only

FIGURE 1.1 An example of the challenges facing the plant taxonomist is shown dramatically by this bizarre landscape, which could represent an obscure area of the earth or perhaps even another planet, with completely new and different plant forms. If this scene were on earth, we would have considerable biological information on modes of reproduction, structures, functions, etc., in plants in general and a good background of ideas on how to proceed with classification of these groups based upon historical classificatory records. If on another planet, however, to attempt a predictive classification of these forms would be unbelievably difficult, with nothing known about modes of reproduction, structures and their functions, mechanisms of evolution, or even what is an individual or population. This same type of overwhelming challenge was faced by plant taxonomists on this planet approximately 500 years ago. (From Lionni 1977, frontispiece)

do new techniques of data-gathering provide more information that must be brought to bear on understanding relationships, but also these new interpretations reveal new taxonomic groups which must be understood and utilized. These are some of the reasons why taxonomy (and its parent discipline, systematics) has rightly been called "an unending synthesis" (Constance 1964), "an unachieved synthesis" (Merxmüller 1972), or even more poetically, "the stone of Sisyphus" (Heywood 1974).