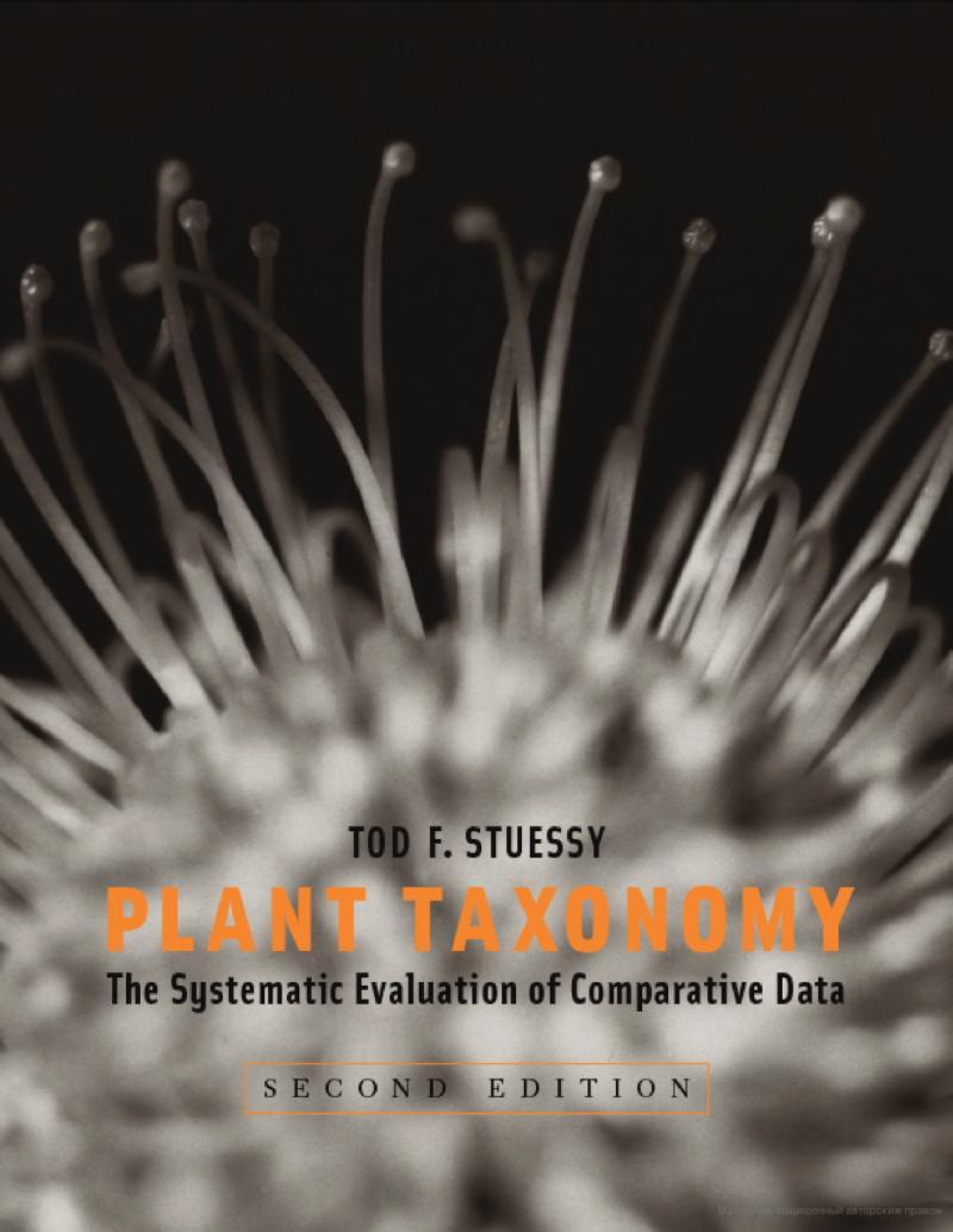

TOD F. STUESSY

PLANT TAXONOMY

The Systematic Evaluation of Comparative Data

SECOND EDITION

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Contents

Preface to the First Edition

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 25 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 are often acrimonious, and the polarization of the broad community of systematic biologists is 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 One 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 when reading this book, 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 Two 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 spans for historically important workers are given to help show the total period in which each individual lived and worked. The literature cited is not exhaustive, but is extensive enough so that most topics are covered reasonably thoroughly, and it can serve as a good springboard for additional readings in a particular area. The cutoff date for new literature additions was 1 July 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.

Columbus, Ohio 1989, T.F.S.

Preface to the Second Edition

Most technical books quickly outlive their usefulness. Published in 1990, the first edition of *Plant Taxonomy*, although still serviceable in many ways, now lacks discussions of new avenues in plant systematics that have appeared during the past 15 years. This second edition attempts to remedy this deficiency.

From a general perspective, these years have seen amazing changes in new data and their utility at all levels of the hierarchy from populations to orders and even to domains. Innovations in use of molecular data, tree-building algorithms, and statistical evaluations have changed the field immeasurably. This has not been a time of deep philosophical reflection that we did in the 1960s and 1970s. The 1990s was a period of experimenting with new data, especially those from DNA, and how best to handle them. The results have been nothing short of extraordinary (some might say even revolutionary), and systematic biology is now viewed as more central to biology as a whole than ever before.

Another remarkable achievement during these 15 years has been the agreement of the systematic biology community on a single highest priority: the complete organismic inventorying of the planet (*Systematics Agenda 2000;* Anonymous 1994). Although this single objective is appealing in its simplicity and obvious in its importance to human welfare, we have not yet been able to marshall needed implementations to achieve this objective. Perhaps the next 15 years will demonstrate success in what is admittedly a more political arena. The new Web-based *Encyclopedia of Life* project offers hope in this direction.

With any second edition, an author obviously must decide on what exactly is the goal. With a brand new text, it is in some ways easier—a new logical structure is formulated, and the volume starts to take shape. This second edition of *Plant Taxonomy* preserves the structure of the first edition and adds to it. This has resulted in some degree of tension in the book, due to so many changes in our field during the past 15 years. I have also elected to leave many of the older literature citations and add new ones to them, hence providing a more than 40-year sweep of references for our field. This seemed to me more useful than eliminating all earlier references and replacing them with only the more modern citations. With new topics, however, such as in the chapters

(21 and 22) dealing with molecular data, I have obviously focused on the recent papers. As for figures to illustrate points made in the text, I have kept many of the previous ones, if they still seemed to communicate the points effectively, but I have also changed and added others (89 new plates) based on the nature of the data and/or visual appeal.

To provide proper literature coverage for this second edition, the following journals were systematically reviewed from 1989–2006: *American Journal of Botany*; *Annual Review of Ecology, Systematics and Evolution (formerly Annual Review of Ecology and Systematics)*; *Cladistics*; *Evolution*; *Molecular Ecology*; *Plant Systematics and Evolution*; *Systematic Botany*; *Systematic Biology* (formerly *Systematic Zoology*); and *Taxon*. The cutoff date for addition of most new literature was 31 Dec 2006, with selected additions up until 1 Oct 2007. Articles from many other journals have also been incorporated, obviously, but these formed the core of the new information. New books have also been consulted, and these have been liberally cited as an aid to the interested reader. Some important, overlooked, older references have also been added for more completeness.

In a text of this broad scope, it is obviously impossible to discuss and analyze all issues in depth. My philosophy has been to provide enough literature citations so that the reader has a basis for consulting the primary literature on nearly any topic. All told, more than 3000 new citations have been added. The objective has been to open doors and windows to the numerous and complex topics in systematic botany rather than to provide detailed analyses for each. Obviously, some topics are covered in more depth than others depending upon my own interests.

This second edition has also provided the opportunity to redress deficiencies in the first edition. Several helpful reviews of *Plant Taxonomy* (Jensen 1990a; Austin 1991; Campbell 1991; Keener 1991; Stevens 1991a; Mabberley 1992; Morrison 1993) have shown the needs to address specific topics in more detail and to correct errors of writing, editing, and production. James Runkle in 1993 also sent me student evaluations of the book that were extremely helpful.

I hope that the revised edition of *Plant Taxonomy* will prove as serviceable as the first. For my part, I have learned an incredible amount regarding new developments in our complex and challenging field. It is not easy being a plant systematist—but I can't possibly imagine being anything else.

Vienna, Austria 2008, T. F. S.

Acknowledgments for the First Edition

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 The 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 keep 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 Two), 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 that generously have given their permissions are: A. A. 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 Publishing Co., 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 Publishing Co., Champaign, IL; 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*; John Wiley & Sons, New York; *Kew Bulletin*; *Madroño*; McGraw-Hill Book Co., 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, NJ; *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 of Kansas Press, Lawrence; University Park Press, Baltimore; W. H. Freeman and Co., San Francisco; W. Junk Publishers, The Hague; Wadsworth Publishing Co., Belmont, CA; and Willliam Collins Sons & Co., London. Permission was also granted by the British Museum (Natural History) to reproduce Fig. 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 was published in Stuessy (1989).

The editors of Columbia University Press were extremely helpful with 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 his staff, a much higher level of quality has been achieved in this book than would have been possible solely through my efforts.

Extremely significant persons in this undertaking have been John W. Frederick; Jonathan Abel; and my wife, Patricia. John entered the original typescript on computer-readable diskettes, thereby facilitating the subsequent revisions. He also checked the quotations and literature citations against the original works. Jonathan Abels and my wife, Patricia, helped check inconsistencies between the text citations and the Literature Cited.

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 Jun Wen, Thomas Lammers, and James Zech. Without this constant prodding, I doubtless would never have finished the task.

Acknowledgments for the Second Edition

As with the first edition, many people have helped make this second edition possible. Most important is Alice Luck, who carried out the copying of the selected literature and typed numerous drafts of the manuscript. She was followed by Walter Sontag, who continued with this same aid, plus helping with organizing the final complete manuscript and integrating the old and new literature citations. Alessandra Lamonea and Monika Paschinger also typed portions of the manuscript. Franz Stadler scanned and formatted the plates. Thanks also go to Franz for skillfully preparing the indices, which add so much to a book of this complex nature.

Many friends and colleagues generously read chapters and made many helpful suggestions for improvement. These are: Christiane König (Chapter 7); Gerald Schneeweiss and Mark Mort (Chapter 8); Anton Weber (Chapter 15); Veronika Mayer (Chapter 16); Johannes Greilhuber (Chapter 17); Michael Hesse (Chapter 18); Karin Vetschera (Chapter 19); Hanna Schneeweiss (Chapter 20); Dan Crawford and Rose Samuel (Chapter 21); Josef Greimler and Peter Schönswetter (Chapter 22); and Elvira Hörandl (Chapter 23).

Permissions to reproduce the new figures in the book have been obtained from the authors of the articles as well as publishers of the following journals: *Aliso, American Journal of Botany, Botanical Journal of the Linnean Society, International Journal of Plant Sciences, Journal of Plant Research, Polish Botanical Studies, Systematic Botany, Taxon,* and *Tropische und subtropische Pflanzenwelt*. Permission to use one book figure was provided by Science Publishers, Enfield, New Hampshire.

Most important have been the editors of this book. At Columbia University Press, Patrick Fitzgerald and Marina Petrova provided efficient, productive, and satisfying help. Eileen Schofield copy-edited the entire manuscript with outstanding critical precision. Kay Burrough of The Format Group, Austin, Texas also provided excellent attention to production of the final volume.

Taxonomy provides the bricks and systematics the plan, with which the house of the biological sciences is built.

(R. M. May, 2004:733)

Taxonomy can justly be called the pioneering exploration of life on a little known planet.

(E. O. Wilson, 2004:739)

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

(L. Constance, 1957:92)

Plant Taxonomy

PART ONE

Principles of Taxonomy

SECTION 1

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 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, chemistry, and molecular biology. 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 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 that 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).

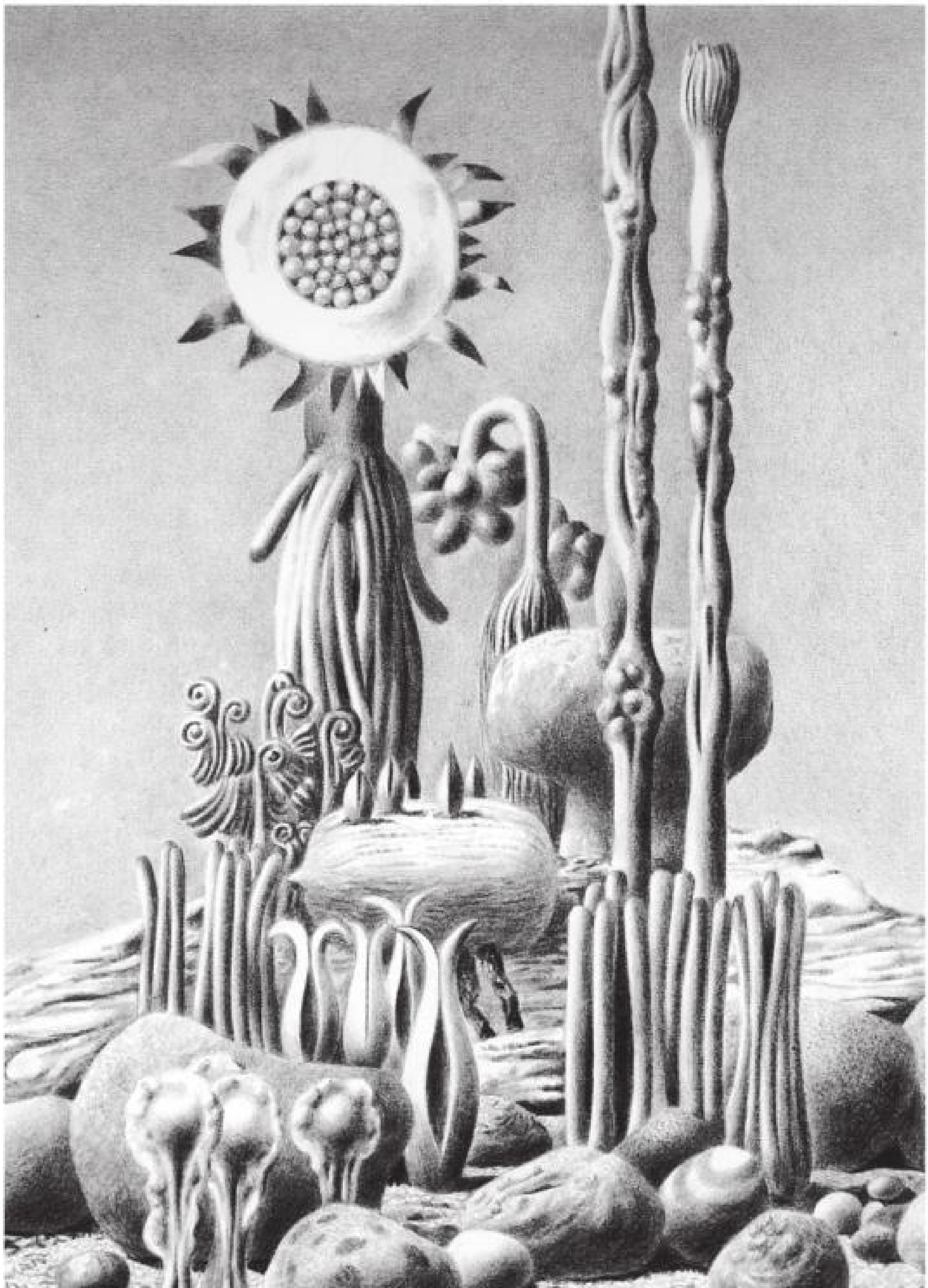

FIGURE 1.1 An example of the challenges facing the plant taxonomist is shown dramatically by this bizarre landscape, which could represent an obscure area of the earth or perhaps even another planet, with completely new and different plant forms. If this scene were on earth, we would have considerable biological information on plants in general, e.g., modes of reproduction, structures, and functions, 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, attempting 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)

CHAPTER 1

A Few Definitions

Classification, Taxonomy, and Systematics

Taxonomy has had various meanings over the past 150 years, and particular confusion with systematics has prevailed. Systematics no doubt was used very early as "a casual self-evident term" (Mason 1950:194) to refer to the ordering of organisms into rudimentary classifications. This activity has occurred ever since people have lived on earth (Raven, Berlin, and Breedlove 1971). The early documented use of the term *systematics* (as systematic botany) can be traced at least as far back as Linnaeus (1737a, 1751, 1754), and it has persisted to the present day although in modified form. Linnaeus (1737a:3) stated that "we reject all the names assigned to plants by anyone, unless they have been either invented by the Systematists or confirmed by them." In 1751, he used the term (as "botanico-systematici," p. 17) to refer to workers who "carefully distinguish the powers of drugs (in plants) according to natural classes." He made the definition of a Systematic Botanist even more clear in his preface to the fifth edition of the *Genera Plantarum*:

> The use of some Botanic System I need not recommend even to beginners, since without system there can be no certainty in Botany. Let two enquirers, one a Systematic, and the other

> an Empiric, enter a garden fill'd with exotic and unknown plants, and at the same time furnish'd with the best Botanic Library; the former will easily reduce the plants by studying the letters [i.e., features of diagnostic value] inscribed on the fructification, to their Class, Order, and Genus; after which there remains but to distinguish a few species. The latter will be necessitated to turn over all the books, to read all the descriptions, to inspect all the figures with infinite labor; nor unless by accident can be certain of his plant" (1754:xiii, 1787:lxxvi).

Books using the term *systematic botany* appeared thereafter (e.g., Smith's *An Introduction to Physiological and Systematical Botany* 1809 and Nuttall's *An Introduction to Systematic and Physiological Botany* 1827). Mason, although admitting the difficulty of establishing the place of its first use, ventured the opinion that systematics "might possibly have even preceded it" [i.e., the use of taxonomy] (1950:194) and gave Lindley (1830b) as the earliest reference.

A biologist interested in relationships during this early period mostly studied morphological features and accordingly grouped organisms into units. This ordering of organisms into groups based on similarities and/or differences was (and still is) called *classification*. This is a very old term going back to Theophrastus in the third century B.C. (see 1916 translation). The Swiss botanist, Candolle (1813), in the herbarium at Geneva, coined *taxonomy* (as taxonomie)[1] to refer to the theory of plant classification. It later became more generally used for the methods and principles of classification of any group of organisms and is still used basically in this way (e.g., Simpson 1961). From this point to the publication of the theory of evolution by means of natural selection by Darwin (1859), the two words, *taxonomy* and *systematics*, were regarded as synonyms, although the latter was used much more frequently. During this time, classifications were believed to reflect the plan of natural order created specially by God, and man was simply rediscovering the Divine Plan. Biologists engaged in these activities of classification were called interchangeably either taxonomists or systematists. Since Darwin's time, systematists have not only continued their interest in classification, but also have attempted to understand evolutionary relationships among the groups so ordered. Furthermore, some systematists have become interested in the process of evolution itself, that is, in the mechanisms that produce the diversity. Consequently, a systematist today may study many different aspects of evolutionary biology that are far removed from the morphological investigations of a century ago. For a useful overview of themes and progress in plant systematics during the past half-century, see Stevens (2000a).

The basic methodology of modern systematics is outlined in table 1.1. Data are gathered from organisms and their interactions with the environment and used to answer questions about classification, phylogeny, and the process of evolution. Specific examples of systematic studies might be analyzing the patterns of adaptive radiation within a particular group of species, comparing DNA sequences for reconstruction of phylogeny, or investigating patterns of intra- and interpopulational genetic variation. A similar and equally legitimate viewpoint was presented by Blackwelder and Boyden (1952), who indicated three steps: (1) recording of data; (2) analysis of the data for making classifications; and (3) synthesis of

Table 1.1 Outline of Methodology of Systematics

I. Accumulation of Comparative Data
    A. From the Organism
        1. Structures
        2. Processes (interactions among structures)
    B. From the Organism-Environment Interactions
        1. Distributions[a]
        2. Ecology
II. Use of Comparative Data to Answer Specific Questions
    A. Classification (most predictive system of classification at all levels)
        1. Method and result of grouping of individuals
        2. Level in the taxonomic hierarchy at which the groups should be ranked
    B. Process of Evolution
        1. Nature and origin of individual variation
        2. Organization of genetic variation within populations
        3. Differentiation of populations
        4. Nature of reproductive isolation and modes of speciation
        5. Hybridization
    C. Phylogeny (divergence and/or development of all groups)
        1. Mode
        2. Time
        3. Place

[a] Floristics, or the documentation of what plants grow in particular regions, is deliberately not listed in this table as a separate question, nor does it find a specific place in the areas of systematics in figure 1.2. Determining where particular plants grow is a very legitimate and valuable activity within systematics, but it is essentially data-gathering of distributions of plant groups that have already been classified. Some floristic projects, however, especially of poorly known regions (e.g., Rzedowski and McVaugh 1966; McVaugh 1972a, b) involve considerable amounts of classification as well as original historical scholarship. To this extent, they become more revisionary, and less floristic, in character (for these and other distinctions, see Stuessy 1975). Many innovations in floristic work are presently occurring, especially using Web-based technologies (see symposium introduced by Kress and Krupnick 2006).

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[1] Some workers, e.g., Richter (1938), believed that taxonomy, if properly derived from its Greek roots, should be spelled "taxionomy" (or even "taxinomy"), but these suggestions for change were unfounded and unnecessary (Mayr 1966; Pasteur 1976) and have never been adopted.

and Elisens 2001), which utilizes different types of data and the computer to help reveal relationships.

The label *new taxonomy* was used by Cain (1959a) to refer to anticipated advances in making taxonomic comparisons by more quantitative means. This hope did not materialize in the way Cain envisioned, but the development of what eventually was called *numerical taxonomy* has yielded many useful results (see Chapter 7). Cain also introduced the term *cryptic taxonomy* (1959b) or *cryptotaxonomy* (1962) to refer to taxonomy in which the exact features used for comparisons have not been made explicit (i.e., most of the traditional intuitive approaches). The new taxonomy was meant to remedy this.

Comparative Biology

Comparative biology, also sometimes called "the comparative method" (Fisher and Owens 2004), is a term similar to systematics and regarded as synonymous by some (e.g., Nelson 1970). I view it here as broader, embracing any study that compares particular features of organisms. For comparative biology to be equivalent to systematics involves the asking of questions only about classification and/or evolution (table 1.1). But other very different questions also are sometimes asked that utilize comparative data for answers, such as in genetics, physiology, or descriptive and developmental anatomy. The focus of these studies is simply descriptive of form and/or function and not interpretive in the context of evolutionary relationships. It is probably true that the most meaningful questions answered with comparative data are, in fact, systematic ones, which may be one of the reasons why some workers (e.g., Mayr 1969c) regarded comparative biology as falling completely within systematics. Another and more broad approach was taken by Nelson and Platnick (1981), who regarded comparative biology as "the science of diversity" (1981:5), which includes the primary areas of systematics and biogeography and also the secondary areas of embryology and paleontology.

tion of global conservation efforts (Brooks et al. 2006; Wilson et al. 2006). Elimination, or at least amelioration, of poverty also relates to successful initiatives for biodiversity conservation initiatives (Adams et al. 2004), as does reduction of corruption (R. J. Smith et al. 2003; Laurance 2004). Hedberg stressed: "In a world with rapidly increasing human population pressures and accelerating exploitation it is imperative to utilize biological resources sagaciously on a sustained yield basis, and to this end we must have an adequate knowledge of its flora" (1978:7). Many species yet to be described will have enormous value for food and medicine, and these are often encountered serendipitously in the course of general floristic work or in field work primarily devoted to other purposes (Iltis 1982). Systematics is essential for helping ensure our continued survival on this planet (Forey et al. 1994; Vane-Wright 1996; Leadlay and Jury 2006).

There is very good recent news with regard to systematists and conservation in that for the first time in history, the systematic biology community has come together to support a single top priority: to provide a complete biotic inventory of the planet, the well-known *Systematics Agenda 2000* (Anonymous 1994). However remarkable this written consensus is, still lacking is translation of community consensus into funded reality, such as achieved by astronomers or high-energy physicists with their pieces of equipment with multimillion- or billion-dollar price tags. Positive steps toward implementation can be seen with the ALL Species Foundation project (Smith and Klopper 2002; Boom 2005), which aims to inventory all life forms within approximately 25 years. There is also now the Web-based *Encyclopedia of Life*, which is user-contributed and so may have a better chance to succeed.

Despite centuries of systematic work, we still know perhaps only 80 percent of the seed plants, 5 percent of the fungi, and an even smaller percent of the microbial world. We are still quite clearly on a new voyage of discovery of our own planet (Donoghue and Alverson 2000; Prance 2001; Brooks and McLennan, 2002). There is even considerable disagreement on the number of seed plants that inhabit the earth, i.e., the dominant vegetation, with estimates ranging from a low of 223,300 (Scotland and Wortley 2003) or ca. 260,000 (Thorne 2002) to more than 420,000 (Govaerts 2001, 2003; Bramwell 2002).

Clearly much more collecting is needed (Prance 2001, 2005), as is more monographic work (Stuessy 1993; Helgason et al. 1996; Hopkins et al. 1998; Kirschner and Kaplan 2002). Considerable attention has been given to the "taxonomic impediment" (Environment Australia 1998), i.e., the lack of trained personnel to get the job accomplished. While the lack of human resources is certainly an issue, employment of parataxonomists, those with some training, may provide a solution (Basset et al. 2000). Likewise, U.S.A. governmental funds have also been channelled successfully toward large training programs in monographic systematics (the PEET program; Rodman and Cody 2003). Certainly greater use of the Internet in making information on existing biodiversity more readily available is also to be encouraged (Bisby 2000; Godfray 2002; Wheeler 2004).

As a result of the need to inventory the planet, especially considering the current high rate of loss of biodiversity, some workers (Blaxter 2003; Tautz et al. 2003; Pons et al. 2006) have suggested completing a more rapid DNA inventory rather than a relatively time-consuming, normal, taxonomic approach of defining and describing new species based largely on morphological features. As one example, Fuhrman and Campbell (1998) found DNA sequences from deep-sea samples that were 30 percent different from any known organism. As another example, Venter et al. (2004) filtered several hundred liters of sea water from the Sargasso Sea, not known for its microbial diversity, and used whole-genome shotgun sequencing to reveal the existence of microorganisms. The results yielded 148 previously unknown "phylotypes." Others have echoed the need for similar microbial assessments (DeLong and Pace 2001; DeLong et al. 2006; Mering et al. 2007; Not et al. 2007). Positive suggestions for inventorying fungi in the soil have also been expressed (Gewin 2006). Although such efforts tell us next to nothing about the organisms themselves, i.e., about their morphology, reproduction, life processes, and ecology, they can show levels of genetic diversity within a particular ecosystem. Some overly enthusiastic workers, however, have even advocated establishment of classifications based primarily on DNA sequences (Tautz et al. 2003; Blaxter 2004), but not surprisingly, not everyone agrees (Seberg et al. 2003). Moritz (2002) and Ennos, French, and Hollingsworth (2005) have properly stressed the importance of thinking not just about conserving taxa (or structures) but also about evolutionary processes, especially in dynamically changing taxa that provide us with difficult taxonomic boundaries.

Systematics can also help in developing further the economic resources that we already have. Biological control of agricultural pests, especially insects, has been used for decades with frequent success. For such endeavors to work well, systematists must be involved with proper identification of the organisms plus supplying data on their ecology and reproductive habits (Clausen 1942; Sabrosky 1955; Rosen 1986) to avoid unanticipated, unwanted, and economically ruinous results. Proper identification of plant materials is also important in customs work, as well as forensic applications (Coyle 2004). The proper use of land resources such as the building of new dams, new canals, and strip mines, is another area in which systematists play an indispensible role by advising on the possible ecological impact on organisms living in the region (Hedberg and Hedberg 1972). Further, the knowledge and techniques gained by systematists through study of relationships of wild species can often be used to improve

CHAPTER

3

The Importance and Universality of Classification

Of the numerous important contributions that systematics makes to society and biology, none is more significant than that provided by classification (and its theoretical and methodological umbrella, taxonomy). Classification is a pervasive human quality "like the predisposition to sin, it accompanies us into the world at birth and stays with us to the end" (Hopwood 1959:230). Although it cannot be denied that the construction of classifications provides intellectual satisfaction for those who make them (J. A. Moore, in Warburton 1967), and, in my opinion, this by itself is justification enough, many more positive features of classification also exist. Heywood suggested that the societal value of taxonomists and their classificatory efforts and products would be negligible: "what effect would a strike of taxonomists have? The immediate effects would be few! A handful more people would die each day as the narcotics bureaus and emergency hospital services were unable to identify plant material;

some hierarchies reflect more of these relationships than others. A minority viewpoint is that because we shall never know any true phylogeny (which must be admitted as a fact of life), then we shouldn't waste time trying to reconstruct one (Sokal and Sneath 1963), and we shouldn't delude ourselves into believing that our classifications really reflect these evolutionary patterns in any precise way (Davis and Heywood 1963; Davis 1978; Brower 2000a). I do not share this perspective.

Another most significant feature of classifications is their use as summarizing and predictive devices (Rollins 1965; Warburton 1967). This is mentioned by most workers as the most important quality of a classification, but it is often phrased in slightly different ways, e.g., "to construct classes about which we can make inductive generalizations" (Gilmour 1951:401; see his similar view in 1940), or "as a basis for predicting a maximum number of unknown characters" (Michener 1978:114). It is worth bearing in mind, however, that "The idea of the predictive value of a classification is ambiguous. It means that one can describe a trait as characteristic of all members of a taxon before it has been verified for all. It also means that if organisms have been classified together as a taxon[1] because they have all been found to share certain traits, they will later be found to share other traits as well" (Warburton 1967:242). An example of the first meaning of prediction is the following: consider that within class A, defined by features other than leaf arrangement, members of subclasses X and Y are discovered to have opposite leaves. We can infer, therefore, that members of a third subclass Z in the same class should also have opposite leaves. To test this prediction in an informal sense, we can look at Z and see what type of leaf arrangement it has. To test the prediction even further, we can look at the leaves of the most distantly related subclass that is still included within class A. The ability to make such predictions is the basis for much of our search for useful plant materials, especially for chemical compounds that have medicinal value ("bioprospecting;" e.g., Balick, Elisabelsky, and Laird 1996). If a useful compound is discovered in one group of plants, the most closely related groups are looked at next to learn if they, too, might have the same or similar compounds. As an example of the second meaning of prediction, continuing the same example as above, if within class A subclasses X, Y, and Z all have certain morphological and anatomical features the same, then one can predict that their chemical constituents (or lack of them) will be the same, too, even though nothing is yet known about this type of data in this group. Warburton stresses the importance of the predictive value of classification: "All other biologists must trust taxonomists to provide them with classifications that maximize this probability [of inductive generalizations], since the validity of all observational and experimental biology depends upon such classifications" (1967:245).

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[1] The term taxon refers to a taxonomic group at any rank in the hierarchy, such as species, genus, or family (coined by Meyer-Abich 1926; see also Mayr 1978). The term will be covered later in this book in our discussion of categories, but it is so useful that its early introduction here facilitates discussion in this and subsequent chapters.

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1986, for additional agreement). Mayr (1969c) pointed out that historically in systematics, the term character had been used in this way for centuries, whereas the concept of character state had been only recently introduced explicitly (Michener and Sokal 1957; Cain and Harrison, 1958, also used character "value" in the same context). He advocated return to the original usage (as did Blackwelder 1967a).

Other workers have agreed with this perspective, but not for historical reasons. Those who strive to construct classifications based on explicit ideas of relationship by evolutionary descent and rigidly devised rules, the "evolutionary cladists" (to be discussed fully in Chapter 8), view a character as "a feature of an organism which is the product of an ontogenetic or cytogenetic sequence of previously existing features, or a feature of a previously existing parental organism(s). Such features arise in evolution by modification of a previously existing ontogenetic or cytogenetic or molecular sequence" (Wiley 1981a:116). From this perspective, only characters have information of evolutionary value for constructing classifications, and the need for states vanishes. Eldredge and Cracraft also argued that use of character state is unnecessary because character and character state are seen as relative terms and "should be construed to mean relative levels of similarity within a given hierarchy" (1980:30). The "theoretical cladists," also called "transformed cladists" (Hull 1984), or "pattern cladists" (Brady 1985), who viewed classification systems primarily as informational and organizational systems without direct evolutionary implications, took an even broader view of a character as "a unit of 'sameness'" (Platnick 1979:542). Ghiselin (1984) even suggested abandoning character and character state and using "feature" for both, but this would be terribly destabilizing (see below) and is not at all recommended.

Related to character and character state are several other general terms that need to be discussed, such as attribute, quality, feature, trait, characteristic, descriptive term, property, accident (accidentia), difference (differentia), and essence (essentialia). These descriptors are all somewhat related and will be considered within the context of three general viewpoints: philosophical (or epistemological, which deals with the theory of the origin, nature, and limits of knowledge); logical; and biological. Very generally, a *feature* is defined in dictionaries as "a prominent part or characteristic" (Mish 2003:458). In a philosophical context, Griffiths (1974a) treated character and attribute as synonyms and defined them following Kant (from Abbott 1886): "An attribute is that in a thing which constitutes part of our cognition of it;" and "a partial conception so far as it is considered as a ground of cognition of the whole conception" (quoted in Griffiths 1974a:108). An *essence* (essentialia) is a feature that attempts to reflect the philosophical essence of an object, as used in Plato's essentialist philosophy (discussed earlier). *Trait* in my view would be a synonym for attribute or feature. Nixon and Wheeler (1990), however, drew a distinction between trait and character state. They regarded the former as an attribute that is not distributed among all individuals of a terminal evolutionary lineage (clade) and the latter as one that is comprehensively distributed (and hence of greater systematic import). The logical viewpoint, deriving from traditional Aristotelian logic and represented clearly in the works of Linnaeus (Cain 1958) and other early classifiers, distinguished among difference (differentia), property, and accident (accidentia). In a strict logical sense, "Any quality or attribute is regarded as being either a difference or a property or an accident. A quality is said to be a *difference* if it serves to distinguish the class of entities of which it is a quality from other species of the same genus [genus and species used here in a logical sense of set and subset relations], i.e., if it is utilized in the definition of the class. A quality is said to be a *property* if it is a quality necessarily possessed by every member of the class, yet not utilized to distinguish the class from other species of the same genus. A quality is said to be an *accident* if it may indifferently belong or not belong to all or any of the members of the class" (Sinclair 1951:94–95; for a historical discussion of how the seventeenth century taxonomist, John Ray, viewed accidents, see Cain 1996). Within the biological context, a *characteristic* is viewed as: "A particular character state occurring exclusively in certain specimens or species. . . . Thus concerning the character *tail*, *bushy tail* is a characteristic of squirrels and *scaly tail* is a characteristic of rats. *Bushy* and *scaly* are different states of the character *tail*" (Ross 1974:20). A *descriptive term* is a descriptor referring to a condition (or state) of an organism that has taxonomic import, and it can be equated with characteristic in the sense of Ross (1974) above. In summary, then: difference, property, accident, and essentialia have precise logical definitions; feature, quality, and attribute all refer generally to some aspect of an organism (whether taxonomically useful or not); and characteristic and descriptive term refer to aspects that are regarded as taxonomically significant.

A good closing perspective to this discussion of definitions of general characters and related terms is provided by Davis and Heywood: "It follows from what we have just said that no precise general answer can be given to the question 'what is a character?' This can only be considered in individual cases and what we treat as a character will depend on what we want to use it for. Even apparent absence of differential characters or expressions between individuals or groups need not indicate that they are identical: differences may well come to light after detailed study. It has been remarked that one will always find characters for separation if one tries hard enough and, one might add, find that characters used for separation do not hold when more material is examined!" (1963:114).

de Pinna (1991) similarity and congruence. Suffice it to say that detection of homologous characters is a difficult problem for any phylogenetic reconstruction, and pitfalls can occur (see the problem of interpretation of leaf homologies in *Acacia*, in Kaplan 1984). Developmental genetics offers many potentials (Jaramillo and Kramer 2007). Because of the complexities of the issue, botanists have tended to deal with the problem obliquely, as indicated by Stace: "Homology is usually defined on the basis of common evolutionary origin, a definition which should in theory be uncontentious, but which in fact is usually quite impractical because of our lack of evolutionary data. In practice, therefore, one can only guess at homologies by making as detailed as possible an investigation of the structures concerned. More usually the problem is ignored" (1980:55). Wiley (1981a) recognized three types of characters: structural, functional, and phylogenetic. The first two are those that *appear* to be similar, but are actually analogous. His phylogenetic characters are the only true homologues. This is a confusing perspective, because the way to determine homologies (or his phylogenetic characters) is in part through detailed structural (or even functional) comparisons.

Other sets of terms also are applied to phyletic characters. *Phylogenetic* and *ontogenetic characters* are simply features that, respectively, are presumed to reflect information about the phylogeny of the group and deal with developmental features. Ontogenetic sequences can suggest phylogenetic patterns, but they may not always do so (to be discussed in more detail later). A *regressive character* is one in which loss of appendages or other features has occurred (Mayr 1969c), such as absence of roots in some aquatic angiosperms (e.g., *Ceratophyllum*, Ceratophyllaceae). Use of this type of character requires caution so as not to confuse it with the original absence of a feature. In the evolutionary context, it is common to speak of *adaptive* and *nonadaptive characters*. An adaptive feature is one that contributes to the fitness of an organism (i.e., its ability to leave offspring successfully), whereas a nonadaptive feature does not contribute to fitness. The extent to which characters are adaptive is a contentious issue that is not likely to be easily resolved. The extremes range from viewing all characters as adaptive to the persistence of some percentage of neutral traits, which neither aid nor detract from fitness. Part of the difficulty lies in agreeing on an acceptable definition of "adaptive."

Cladistic Characters

Cladistic characters have developed from the cladistic approach to classification, which attempts to determine branching sequences of evolution and base a classification upon them (see Chapter 8). These branching patterns are revealed through analysis in taxa of distributions of character states that are believed to be significant evolutionarily and contained within homologous characters. A further point is that *only* derived character states are regarded as significant cladistically; primitive conditions are viewed as misleading and uninformative. The pros and cons of this viewpoint will be discussed in detail later in this book, but terms often used in this approach are *primitive* vs. *derived character states*, or as synonyms, *general* vs. *unique*, *generalized* vs. *specialized*, *primitive* vs. *advanced*, *plesiotypic* vs. *apotypic*, and *plesiomorphic* vs. *apomorphic*. The latter terms are those introduced (Hennig 1966) and used by cladists (see Wiley 1981a and Wagner 1983, for good definitions of these and other cladistic terms). Shared derived character states between and among taxa are called *synapomorphies* (or *synapotypies*), and shared primitive states are *symplesiomorphies* (or *symplesiotypies*). An *autapomorphy* is a derived character state occurring only in one evolutionary line and, thus, of no direct use in constructing branching sequences (because only one taxon has the feature). *Polymorphic characters* are those that have variable states within a taxon, and this can cause problems with data coding for cladistic (and phenetic) analysis (for a good review, see Wiens 1999). Characters that are useful cladistically are sometimes called *compatible characters* (Estabrook 1978), in which the evolutionary directionality of the states within each character is the same. Estabrook, Johnson, and McMorris (1975) made the distinction between *true cladistic characters* in an idealized sense and those that are defined operationally in the course of actual studies. This distinction has philosophical validity and mathematical reality, but is of only passing interest for practicing taxonomists.

Phenetic Characters

Another major approach to biological classification is *phenetics*, which uses overall similarity to assess relationships (often referred to as *numerical taxonomy*), and specialized types of phenetic characters have also been proposed. Phenetic classification makes no attempt to reflect evolution; taxa are related based on similarity and difference of character states regardless of the evolutionary content of the characters and states. Much stress in phenetics has been on precision of operations in the process of classification. Therefore, characters are defined in such a way to avoid any circularity as seen earlier with the concept of homologous characters. The character of choice in phenetics is the *unit character*: "a taxonomic character of two or more states, which within the study at hand cannot be subdivided logically, except for subdivision brought about by changes in the method of coding" (Sokal and Sneath 1963:65; the term apparently first used by Gilmour 1940:468). The search for unit characters is based on avoiding logical circularity and obtaining data in which each datum represents a new item (or bit) of information (Sneath 1957; Sokal and Sneath 1963; Sneath and Sokal 1973). These unit

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Practical Considerations

The final perspective on selection of characters and states focuses on practical matters. Despite all the above criteria, there are clearly inconsistencies in how workers deal with and code character data. Hawkins (2000) focused on how multistate characters are coded. She found nine different codings, including nominal variable, composite, ratio, logically selected, conjunction, and positional. Similar investigations also revealing inconsistency have been completed by Forey and Kitching (2000) and Reid and Sidwell (2002). As all practicing taxonomists well know, it is important theoretically to be aware of, and conversant about, ways in which characters are important and can be selected, but basically it comes down to choosing characters "which work" (Cronquist 1957, 1964). We rarely know the genetic, adaptive, evolutionary, or information content of characters routinely used in constructing classifications. The practicing taxonomist does make an assessment of the conservative nature of characters, in the sense of intuitively assessing their variations within and between populations, and looks for correlations with other characters to establish the suites needed for taxonomic circumscription. Pheneticists stress no conscious selection of characters, but rather the use of all of them after proper reduction to their "unit" natures (Sneath and Sokal 1973). However desirable this might be in theory, it is not possible to take this approach with the majority of taxonomic efforts in which speed of work is valued. Selection of a handful of constant characters and constructing a classification from them is much more efficient than carefully reasoning out all the unit characters, which could number more than 100, and developing the classification along these lines. The selection of character states is equally problematical in practice, and this issue has not yet been addressed satisfactorily. The choice of whether to use qualitative or quantitative states is an initial and fundamental problem, although tradition in the taxonomic history of a group offers a guide. But further problems abound: "If a character is to be measured, what set of values should be used to record the state of the character in a given individual? For continuous characters such as leaf length, it might be the nearest millimeter or the nearest centimeter. More difficult decisions involve qualitative attributes, such as leaf shape. Here, an investigator's operational procedure would be simply to recognize those patterns as distinct that best serve the purpose of his analysis. This rule sounds terribly suggestive and unscientific, but, to determine character states for qualitative characters, no formal decision function exists that considers one's material and purpose any better" (Crovello 1974:458).

SECTION 2

Different Approaches to Biological Classification

During the past 50 years, two new efforts toward classification have been advocated: phenetics and cladistics. These have been nothing short of revolutionary in the sense that they have forced us to think about what we really are doing in classification and to do it quantitatively (Stevens 2000a; Stuessy 2006). A comprehensive discussion of these and ancillary approaches to biological classification is needed, especially because of the breadth of the literature and development of different "schools," each with definite (and sometimes dogmatic) viewpoints. Although it is impossible to know everything about all these issues, the student of modern plant taxonomy should be acquainted with, and have an informed personal opinion about, the major points. For an excellent comprehensive review, see Mayr (1982). This section of the book presents brief historical and descriptive accounts of each of the methods, detailed evaluations of the three major approaches (phyletics, phenetics, and cladistics), and a plea for a balanced perspective.

One might make the case that we are now entering a new phase in which schools of biological classification no longer exist. Felsenstein (2004), in fact, suggested this viewpoint. When morphological data were paramount for classification, lots of different perspectives prevailed on how best to use them, especially with quantitative analyses. With the arrival of DNA data, however, especially sequences in the late 1980s and early 1990s, the challenge shifted from arguing about philosophical issues of classification to practical concerns of getting trees for answering specific questions about relationships. That is, the overwhelming new abundance of data forced a more practical attitude toward tree building and classification. For example, with a large dataset of DNA sequences, the use of a phenetic algorithm such as neighbor joining will provide a very fast result and only one tree. With a cladistic parsimony algorithm, it might take hours or days to get a result, and often hundreds of shortest trees are presented, each slightly different. The objective, therefore, has shifted from debates on the philosophical issues regarding procedures in classification to discussions on which kinds and how much molecular data are needed for a convincing view of relationships. Nonetheless, there are still strong views on these issues, and it still makes sense, therefore, to present these different viewpoints separately in this book.

From a historical perspective, Davis and Heywood (1963) recognized in pre-Darwinian classification those systems based on habit, sexual features (the sexual system), and form relationships. The former two are placed here into the artificial approach, and the latter into the natural approach (mostly *a posteriori* systems such as those of Jussieu and Candolle). Jones and Luchsinger (1986) also recognized two additional historical approaches: form and utilitarian. The latter stressed the herbalists' contributions (chiefly artificial), and the former referred only to *a priori* approaches based on external form and, therefore, is also artificial in the context used here. Woodland (2000) recognized form and sexual systems. Other perspectives would include Blackwelder (1964), who championed the "omnispective" approach. This corresponds largely to the natural system as used here, in which selected and weighted characters are used to develop a classification but without emphasis on reconstructing the phylogeny. Kavanaugh (1978:141) mockingly called this the "'trust me, I know what I'm doing' school." All these different perspectives are legitimate alternatives and of interest, but I have organized them here so as not to detract from emphasis on comparison of the three major approaches: phyletics, phenetics, and cladistics. Table 5.1 shows the chronology of these different viewpoints with examples of works primarily from the botanical literature.

classification, as well as being obviously fundamental to artistic endeavors. Kubler (1962:vii) defined art as "a system of formal relations," which could apply equally well to the resultant hierarchy of classes constructed in the process of classification. Simpson (1961:110) treated classification as "a useful art" and spoke of "taxonomic art," in which classification is regarded as a combination of art and science. Mayr offered this perspective: "It is by reading this chapter [Darwin, 1859, ch. 14] that one understands the true meaning of the old saying that classifying is an art. But what is art? To be sure, a superior classification provides a genuine aesthetic pleasure, but the word 'art' in the old saying is used in a somewhat different sense. As in the word 'artisan' it refers to a craft, to a professional competence which can be acquired only through years of practice" (1974a:5–6). Stearn added appropriately: "The work of a taxonomist is closely linked to that of an artist: both seek patterns within diversity, the one to record those he thinks he finds in nature, the other to record those he finds maybe only in his own head, and one person may be both taxonomist and artist, the danger then being that he makes no clear distinction between these two forms of expression!" (1964:84). There are many examples of excellent taxonomists who have also been accomplished artists, e.g., see the personally illustrated works of Hutchinson (1926, 1934, 1969) and Burger (1967). This does not imply in any way, however, that these workers are poorer or more fanciful than nonartistic taxonomists, but rather simply that they have substantial talent in both areas.

Despite the aesthetic ties between classification and art, the former is still unmistakably a science. It is not an experimental science as are chemistry, physics, or molecular biology, but it is science in the sense of description and arrangement of information in an orderly fashion, the development of hypotheses, and the devising of tests to attempt their disproof (and hence invalidation). The descriptive information in characters of organisms is gathered and evaluated and arranged in an orderly fashion into a hierarchical classification, which is the hypothesis of relationships suggested by the data (characters and states). Predictions from this hypothesis involve finding new datasets that will either correlate with (and not disprove) or be inconsistent with (and hence, disprove, or at least suggest reevaluation of) the hypothesis. Tests are made by gathering these new data and comparing their distributions with already extant datasets of other types. Examining newly discovered organisms and learning how all their features compare with those characteristics of already classified taxa in the classification comprise another form of test of the hypothesis. In this fashion, new classifications are often made as new data-gathering techniques become available and as new organisms are discovered through field exploration and museum study.

The close association of the process of classification with art has caused some workers in the past few decades to react negatively. One of the reasons for this negativism may be that science is definitely progressive, whereas art is less so; in fact, the arts have at times been caricatured as a somewhat confused bird "who always flies backward because he doesn't care about where he's going, only about where he's been" (Frye 1981:127). There have been two major efforts to construct classifications on a more objective and repeatable foundation: phenetics and cladistics. In the former, a strong emphasis is placed on the virtues of objectivity and repeatability by taking all characters (unit characters) without subjective selection and by constructing a classification along explicit lines (allowing anyone else to follow clearly what has been done). As Michener and Sokal stressed in one of the earliest phenetic papers: "Taxonomy, more than most other sciences, is affected by subjective opinions of its practitioners. Except for the judgment of his colleagues there is virtually no defense against the poor taxonomist" (1957:159). By the same token, cladistics has developed as a means of revealing branching patterns of evolution more explicitly, and some workers insist that classifications be based directly upon these patterns. "Cladistics has emerged as a powerful analytical tool in comparative biology because it offers most informative (least ambiguous) summations of any set of biological observations represented in a consistent, testable, reproducible framework. Systematics has thus become a truly empirical science, capable of assuming its rightful place as the one indispensable branch of biology—the framework of comparisons for a comparative science" (Funk and Brooks 1981: vi). Despite these laudatory attempts to remove subjectivity, the fact remains that many aspects of classification by whatever approach are still largely based on the sound judgment of the individual worker. The choice of taxa for initial study, the selection of characters, the detection of homologues, and the measurement and description of character states are all aspects that require judgement, creativity, and experience, no matter what approach to classification is used. It is well to keep in mind that these specific areas of uncertainty are backdropped by the general perspective "that science is uncertain in its very nature. With exceptions mostly on a trivial and strictly observational level, its results are rarely absolute but usually establish only levels of probability or, in stricter terminology, of confidence. Scientists must also tolerate frustration because they can never tell beforehand whether their operations, which may consume years or a lifetime, will generate a desired degree of confidence. (If this could be told beforehand, the operations would be unnecessary.) Indeed one thing of which scientists can be quite certain is that they will not achieve a *complete* solution of any worth-while problem" (Simpson 1961:5).

Process of Classification

With all approaches to classification, no matter what the particular bias, the process of classification can be viewed as a series of operations (fig. 5.1). Viewing the classification in this dissected way will facilitate comparison of the different approaches to classification to be discussed next. Earlier in this book, classification was defined as the ordering of individual organisms into groups based on observed similarities and/or differences. When only two or very few groups result from this process, we can treat the resultant units as being coordinate to each other and use the classification system in ways already mentioned. But usually many units are involved, in which case, some method is needed for showing the relationships among the groups, so that we can communicate more easily about part of the ordered diversity. If many units have been created, we face the same problem as if we were confronting many separate individuals. To solve this difficulty, larger groups composed of smaller units are made and given categorical names. In this fashion, a taxonomic hierarchy of ranked units results with the largest units being divided into smaller subunits, these being further divided, and so on. The process of classification, therefore, usually involves two separate operations: (1) grouping and (2) ranking.

Grouping involves three specific steps (fig. 5.1). First, one must select characteristics of the organisms to use in assessing the similarities and differences. It is impossible, in fact, to compare two or more objects without referring to specific features of each (the taxonomic characters). The second step in grouping involves describing and/or measuring these characters. One cannot use the character "leaf shape" for example, to compare two plants meaningfully, because they both have leaves with shape. Instead, the kind of particular leaf shapes in the two plants must be compared, such as "obovate" vs. "lanceolate." These are the character states that are actually used for purposes of taxonomic comparison and evaluation. The third step in grouping is to compare the chosen character states to obtain the groups. These comparisons can be made in different ways. A formal method can be used (such as in phenetics or cladistics), or the comparison can be done more intuitively in traditional approaches. In some situations, particular character states will be regarded as having more importance than others for the particular grouping, whereas in other situations, all the character states will be accorded the same or equal importance. These differences in approach to comparison of character states are important areas of disagreement among some workers regarding taxonomic methodology (to be discussed in detail later).

The second operation in classification is ranking of the recognized groups (fig. 5.1). This involves two specific steps. First, all the character states of the groups are examined, and some are selected for use. The character states might be the same and even include all of those used for grouping, but usually not all of them are used for ranking. Other characteristics also might be selected for consideration that were not used for the grouping. Second, these selected character states of the groups are evaluated in terms of the categories available for use in the taxonomic hierarchy. The presence or absence of certain kinds of features usually will suggest an appropriate rank in the hierarchy of classification. A discussion of the kinds of character states of groups that often are used to indicate certain ranks will be taken up later in Chapters 10 to 14.

A final point worth mentioning is that most practicing taxonomists, although carrying out the operations just described, are not usually conscious of all the different steps. If one were to ask a taxonomist how he or she classifies, the reply might be: "I simply group things together that look similar to me." Although such an answer implies that characters

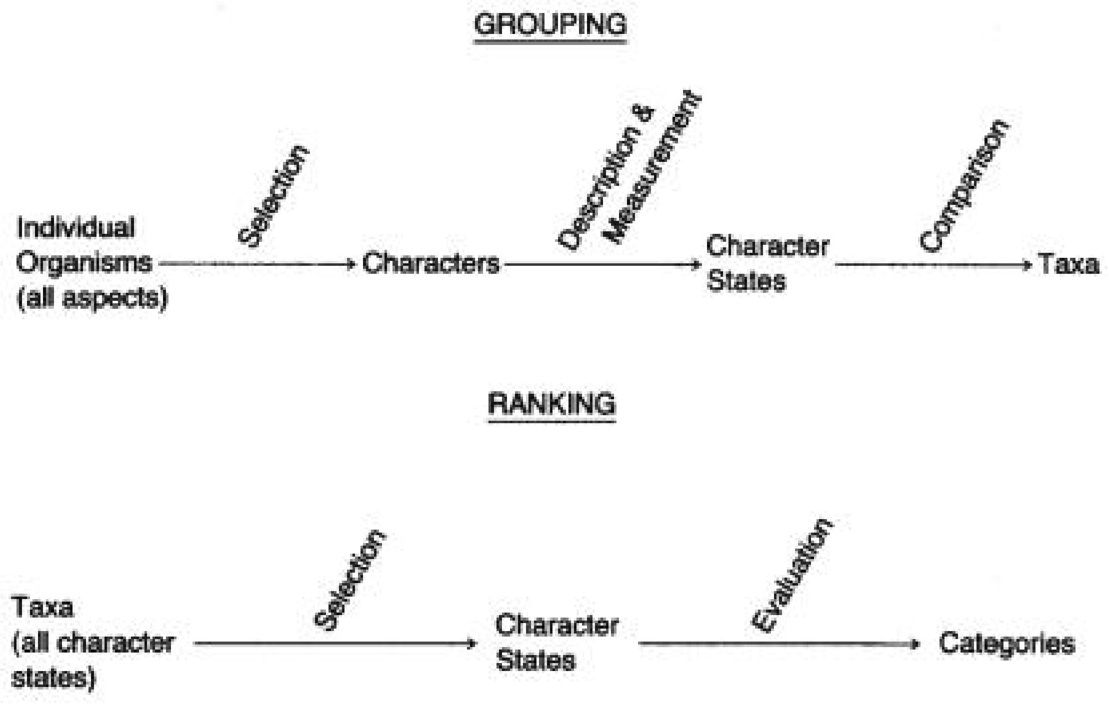


FIGURE 5.1 Representation of the two primary operations of classification. (From Stuessy 1979b:623)

are not selected or character states compared, in reality the taxonomist is unconsciously making many rapid comparisons between features of the organisms selected. With prodding, however, even the most pragmatic of workers can give at least some idea of the specific characters used and compared (many of these are presented clearly in the diagnostic keys that accompany the classification).

Artificial Classification

The artificial approach to classification is that used by most people today for inanimate objects. With this method, only one or at most a few characters are selected for use in making comparisons among objects, and this selection usually is made before the classification is begun (i.e., *a priori*). Because so few characters are involved, the difficulties encountered in describing, measuring, and comparing the character states usually are minimal. Ranking is done subjectively with certain character states being regarded as subordinate to others. The classification systems of libraries serve as excellent examples of the employment of this method. Many libraries have books grouped according to a system of specific subject headings (= character states) that reflect the subject matter (= character) of the organized units. Specific examples of such approaches are the Library of Congress and the Dewey Decimal Systems. These two artificial classifications are based on different sets of subject headings, but they both serve adequately to organize the books in some useful way for proper information retrieval. Other libraries have special artificial classifications ordered by authors' surnames or other subject headings that were designed for specific needs. Most libraries routinely have oversized collections kept in separate quarters simply because of problems with shelving. Rare book rooms provide another example of a unit segregated due to practical considerations, here based on market value and security requirements.

The artificial system was the first to be used for the classification of plants, and these origins in the western world begin with the ancient Greeks (table 5.1). Theophrastus (370–285 B.C.), a pupil of Aristotle, made the first elementary groupings of plants, based on distinctions of habit into trees, shrubs, subshrubs, and herbs in his *De Historia Plantarum* (Enquiry into Plants), translated by Hort, 1916 (see also Pavord 2005). This was followed by the *De Materia Medica* of Dioscorides (ca. 60 A.D.), which was the earliest recorded treatise on the medicinal value of plants. These were largely artificially arranged, but some related plants were grouped together (Core 1955). It should also be mentioned that very early medicinal treatises were prepared in ancient India, for example, the *Atharva Veda* (ca. 2000 B.C.; see Sivarajan 1991), but these had little impact on developments of classification in Europe from which our modern systems have been derived.

With the close of the Dark Ages and the development of the Renaissance (beginning in the fourteenth century), people began again to look firsthand at the living world instead of relying solely on the observations of the ancient Greek writers. During this period of learning and discovery, it was noticed that certain plants had features in common that for one reason or other seemed to be important. Perhaps due to the great suffering inflicted by contagious diseases during this period, a stronger interest was rekindled in the medicinal value of herbs, and these actual or supposed properties formed the basis for organization of the plants into groups. Workers contributing to this interest were called herbalists (from 1470 to 1670) and included many in Germany, Italy, and the Netherlands, such as Otto Brunfels, Hieronymus Bock, Leonhart Fuchs, Andrea Cesalpino, and Rembert Dodoens. These early classifications were artificial because they used only a few characters that related to the presumptive medicinal efficacy of the plants. The important role of the new scientifically (medicinally) oriented botanical garden should also be mentioned (Lack 1998).

From these early attempts by the herbalists eventually came a uniform and stable system of botanical classification. One of the most noteworthy of the artificial systems was developed by the French botanist, Joseph Pitton de Tournefort (1656–1708). He published a comprehensive treatise in 1700, *Institutiones Rei Herbariae*, which dealt with nearly 9000 species of plants in more than 600 genera. His stress on the generic level has earned him the designation as "the founder of the modern concept of genera" (Core 1955:34). Despite its broad coverage, Tournefort's system was still largely artificial with initial emphasis on genera differing in form of the flower and fruit and second-grade genera differing in vegetative features (Davis and Heywood 1963).

The classification (1735, 1753) of the Swedish botanist, Carl Linnaeus (1707–1778), represents the most complete artificial system ever developed for all plants. Linnaeus was impressed by the experimental documentation by Rudolf Jakob Camerer (Camerarius 1694) of the existence of sex in plants and the treatise on that same topic by Vaillant (1718). In fact, in his university days at Uppsala, Sweden, Linnaeus wrote a thesis on the sexual habits of plants, the *Praeludia Sponsalia Plantarum* (1729), and it was undoubtedly this interest that led him to develop his sexual system of classification. Linnaeus placed overriding emphasis on the presence, configuration, and numbers of sexual parts of the flower (i.e., the stamens and carpels). All the flowering plants were placed into 23 "classes" based on stamens, such as *Monandria* (one stamen), *Diandria* (two stamens), and *Triandria* (three stamens). These classes were then divided into "orders" based on features of the carpels, such as *Monogynia* (one style or sessile stigma), *Digynia* (two styles or sessile stigmas), and *Trigynia* (three styles or sessile stigmas) (description from Stearn 1971). This system had the great advantage of allowing all plants to be easily placed in the classification just by looking at these two parts, and even a botanical novice could make the proper dispositions. As a result of its utility as well as of the interest generated by its sexual innuendos (e.g., *Diandria* was described as "two husbands in the same marriage," Stearn 1971), the system became very popular and was accepted virtually worldwide.

TABLE 5.1 Historical Development of the Major Approaches to Biological Classification, with Examples Primarily from the Botanical Literature.

Major approaches to biological classification	B.C.	A.D.	1500	1600	1700	1800	1900	2000
Artificial	Theophrastus[a] → (ca.300 B.C.)		Herbalists → (1470–1670)[b]		Tournefort → (1700)	Linnaeus → (1735)		
				NATURAL			PHYLETIC	
Natural and phyletic			Bauhin → (1623)	Ray → (1686–1704)	Jussieu → (1789) Candolles (1824–73) Bentham & Hooker (1862–83)	Eichler → (1883)	Engler & Prantl (1887–1915) Bessey (1915) Hutchinson (1926, 1934, 1969) Cronquist (1968, 1981, 1983, 1988) Takhtajan (1969, 1980, 1986, 1987, 1997) Thorne (1968, 1976, 1983, 1992a, 2000a, b) Dahlgren (1975, 1980, 1983, 1989a, b)	
Phenetic					Adanson → (1763)		Sokal & Sneath → (1963, 1973)	
Cladistic							Hennig → (1966) APG (1998, 2003)	

Note: For a readable and reasonably detailed account of the history of botanical classification, see Core (1955).

[a] Elements of the natural approach to classification are found in Theophrastus' work, in some of the herbals, and in Tournefort's publications, and even Linnaeus himself produced a sketch of a natural system (1764), also modified and published posthumously by his student, Giseke (1792). Nonetheless, these treatments were largely artificial in contrast to the more obviously natural systems beginning with Bauhin and Ray.

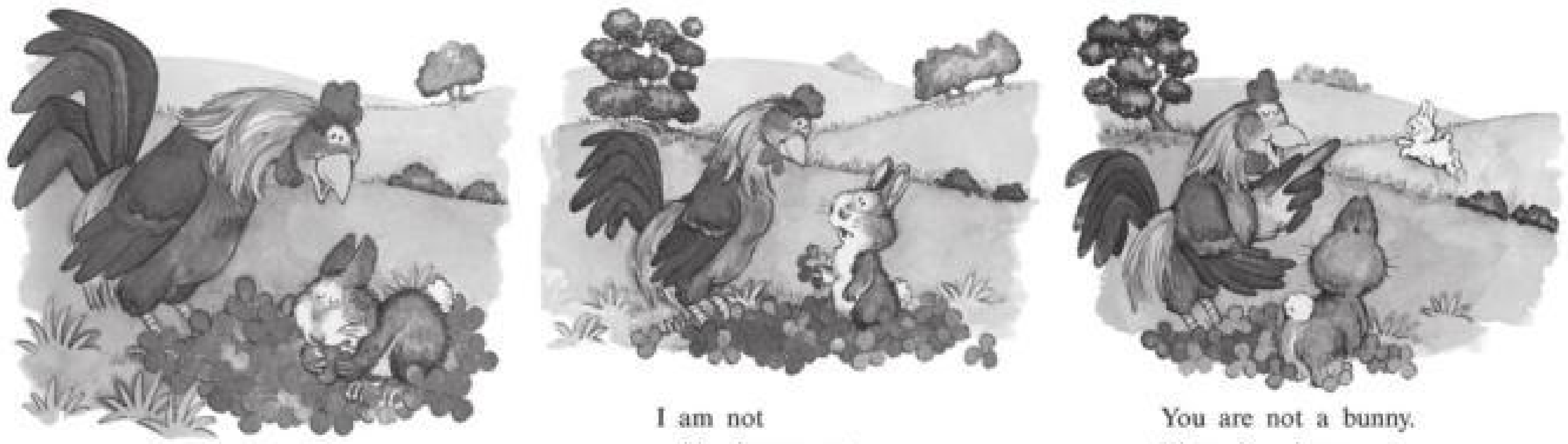
[b] Various inclusive dates for the "Age of the Herbals" exist; those used here come from Arber (1988).

CHAPTER

6

Natural and Phyletic Approaches

Despite the widespread dissemination and acceptance of the Linnaean sexual system of classification, some workers never felt entirely satisfied with it. Although the artificial approach could not fail to allow all plants to be grouped with ease, the resulting groups of plants often seemed very different from each other in regard to features other than the sexual parts (fig. 6.1). Bernard de Jussieu (1699–1777), demonstrator of plants in the Royal Botanical Garden in Paris, arranged the plants in the Royal Garden and in Marie Antoinette's garden in La Trianon at Versailles. Earlier the well-known Tournefort had been in charge of the Royal Garden, and, in fact, Bernard's brother, Antoine, succeeded Tournefort as director. Linnaeus visited the Jussieus in 1738, and the meeting was pleasant, but despite this positive personal contact and the eventual prestige of the Linnaean system, Bernard de Jussieu remained unconvinced. The simple fact was that the sexual system of classification was inadequate for information retrieval and predictive generalization. Bernard attempted to arrange the living plants in the Royal Botanical Garden based upon what he believed to be overall similarity, taking into



Hello,
big, brown rat.

I am not
a big, brown rat.
I am
a little bunny.

You are not a bunny.
There is a bunny.
He is white.
You are brown.
A rat is brown.
You are a rat.

FIGURE 6.1 Example of how emphasis on single characters can lead to completely erroneous artificial classifications of low predictive value. (From DeLage 1978:6-8; drawings by E. Sloan)

consideration as many characters as possible. But he was never completely satisfied with the arrangement and never himself published his system of classification. It fell to his nephew, Antoine-Laurent de Jussieu (1748–1836), who came to Paris as professor of botany in the Royal Botanical Garden, to rework and elaborate upon his uncle's system until it was finally published in 1789 in the *Genera Plantarum Secundum Ordines Naturales Disposita*. This was a most impressive system containing 100 "orders," which corresponded in large measure to our present concept of families, grouped into 15 classes, and these then grouped into three divisions. The characters used to delimit the orders were numerous but included strong emphasis on ovary displacement (epigyny, hypogyny, and perigyny), the suite of characters distinguishing monocots vs. dicots (e.g., parallel vs. net leaf venation; flower parts in threes and sixes vs. fours and fives; absence vs. presence of vascular cambium), and fusion of anthers. In other words, reproductive features were still stressed, as they had been in Linnaeus' system, but they were selected *a posteriori* based upon their ability to result in multiple correlations with states of other characters. For a discussion of the impact of Jussieu, see Stevens (1994, 1997a) and Williams (2001).

Natural Classification

A *natural system* of classification, therefore, is one based upon states of several to many characters selected *a posteriori* for their value in positively correlating with states of other characters to form a hierarchical structure of groups in ranks containing high information content and predictive value. The characters selected, in effect, are weighted by their selection and employment over those features not selected, and this selection and comparison and eventual evaluation (for ranking) are done intuitively by the taxonomist. That is, there is nothing explicit about this process; it occurs rapidly in the mind of the maker (herein lies the aesthetics of the process), and diagnostic characters are usually derived only after the classification is constructed and a key for identification purposes is attempted.

A natural classification is, therefore, *polythetic* (Sneath 1962; from Beckner 1959, as "polytypic"). It "places together organisms that have the greatest number of shared features, and no single feature is either essential to group membership or is sufficient to make an organism a member of the group" (Sokal and Sneath 1963:14). This contrasts with *monothetic* classification, in which groups "are formed by rigid and successive logical divisions so that the possession of a unique set of features is both sufficient and necessary for membership in the group thus defined" (Sokal and Sneath 1963:13). The monothetic quality is characteristic of artificial systems of classification, as exemplified by Linnaeus' sexual system.

It should be noted that even before Linnaeus' time, several workers had begun to struggle with the idea of a more natural system such as Jussieu's, and two are worth special attention (see table 5.1). Gaspard Bauhin (1560–1624) of Basel, Switzerland, produced a compendium of all that was known about plants at that time in his *Pinax Theatri Botanici* (1623; for a good discussion of this work, see Cain 1994). This work was divided into 12 books with further subdivisions, and some similar taxa were grouped together such as genera in the easily recognizable families of Cruciferae, Compositae, and Umbelliferae. Despite this useful beginning, much of the *Pinax* was artificially arranged and had its greatest value as a nomenclator (or register) of all names of plants published prior to that time (encompassing the confusing array of monomials, binomials, and polynomials then in use). The English botanist John Ray (1623–1705) also published the rudiments of a natural system in three volumes of his *Historia Plantarum* (1686–1704). He emphasized habit, monocot vs. dicot distinctions, and other features, and several of the "classes" corresponded to our easily recognizable modern families such as Labiatae, Leguminosae, Cruciferae, and Gramineae.

Despite the existence of these early natural systems, the success of the artificial sexual system resulted from the forceful personality of Linnaeus, his prolific writings, his numerous students who returned to many different countries as his disciples, the ease of comprehending the system, and its sexual overtones. All these factors combined to overshadow the early natural systems of Bauhin and Ray. It wasn't until the early 1800s that the sexual system passed from common use throughout most of the world. In the United States, the sexual system was still in vogue in popular textbooks into the 1830s, when Asa Gray's books provided successful competition using the natural system derived from the works of Candolle in Switzerland (Rudolph 1982). Even though Linnaeus made very impressive contributions to systematic botany and is known as the "Father of Taxonomy," or "*Princeps Botanicorum*" (Core 1955:36), the tremendous success of the artificial sexual system probably retarded the development of the more progressive natural system.

After Jussieu, nearly all subsequent systems of classification were natural until the development of evolutionary reasoning brought about by Darwin's *Origin of Species* in 1859. An important reason for the continued appearance of new, natural, classification systems was the increasing shipments of new plant specimens from little-explored regions of the world, which occasioned a constant reevaluation of plant relationships. Two major natural systems should be mentioned: that of Candolle and that of Bentham and Hooker. The Swiss botanist Augustin Pyramus de Candolle (1778–1841) was trained at Paris and received part of his instruction from A.-L. de Jussieu. Upon completion of his education, he accepted a position as professor of botany at Montpellier and eventually returned to Geneva at the Conservatoire de Botanique where he resided for the remainder of his professional career. His new natural system of classification was presented in the monumental *Prodromus Systematis Naturalis Regni Vegetabilis* (1824–1838), a world flora at the specific level (the last one ever completed, but not including the monocots), the first seven volumes of which were published by him and the remaining ten volumes (1844–1873) by his son, Alphonse (1806–1893). This new system utilized many characters, but it was based upon the foundation laid by Jussieu. George Bentham (1800–1884) and Joseph Dalton Hooker (1817–1911), both working at the Royal Botanic Garden in Kew, England, produced a monumental work of natural classification of all the genera of gymnosperms and angiosperms, *Genera Plantarum*, published in parts between 1862 and 1883. Their system of classification was based on that of Candolle, who was a close friend of Bentham. Numerous morphological and anatomical characters were used, such as numbers of carpels, ovary displacement, nature of perianth, embryo characteristics, and fusion of parts. Despite appearing *after* the impact of Darwin's book on evolution (1859), the project had been started about 1857 and was, therefore, natural rather than avowedly phyletic (i.e., no evolutionary interpretations of any kind were explicitly included). Furthermore, Bentham at the time remained unconvinced of the correctness of Darwin's evolutionary views, but he did accept them later (Bellon 2003; Stevens 2003).

Phyletic (Evolutionary) Classification

The question that constantly arose during the period of development of natural systems of plant classification was why some organisms tended to resemble those of one group more than another. The answer given by some was that the order reflected God's plan of creation, whereas others believed that a natural process must be responsible. Lamarck and many other biologists during the early 1800s believed strongly that evolution, or the process of orderly organic change through time, was perhaps responsible for the observed patterns of diversity. These ideas, however, were not wholeheartedly accepted by scientific colleagues of the day due to lack of an explanation regarding the mechanisms for such a process. It was Charles Darwin (1809–1882) who provided a plausible solution in his book, *On the Origin of Species by Means of Natural Selection* (1859). From that time on, taxonomists had an explanation other than Special Creation as to why their classified groups were homogeneous—they had descended from a common ancestor. Biological classifications ceased to be just storage-retrieval systems; they now also became illustrations of the patterns of evolution. The classification of plants could now be called "phyletic," "phylogenetic," "evolutionary," "eclectic" (McNeill 1979), "synthetic," or "syncretistic" (Farris 1979b). Williams (1996) used the term *gradistic*, but this is inappropriate because the phyletic approach contains a strong cladistic element.

But although an explanation now existed whereby similar individuals were classified together, the theory of evolution by means of natural selection did not alter the process of classification itself (Stevens 1984b). Characters were still selected, described, and measured, and character states were compared as in the natural system. In reality, the process of classification and the resulting hierarchy of classes had not changed. What was altered was simply the understanding of the origin of similarities and differences among organisms. In other words, the philosophical perspective toward hierarchical classifications changed, but not the process itself.

As a result of the emergence of the theory of evolution, therefore, taxonomists began to look at their finished classifications in a different light. Workers began to emphasize relationships by descent of the groups in their systems, and these relationships were often illustrated diagrammatically by phyletic or phylogenetic "trees" (see Voss 1952, for a history of phyletic trees in biology). The rationale for such evaluations involved subconsciously and/or subjectively assigning ancestral or derived status to various character states that allowed groups to be related in a linear fashion from generally more ancestral to more derived. These phyletic assumptions or "dicta" regarding lineages were explicit or implicit in all major phyletic systems (table 5.1).

The first clearly phyletic system of classification of plants was produced by the German botanist, August Wilhelm Eichler (1839–1887). In his book (1883), he dealt with the entire plant kingdom and recognized subdivisions that are still part of our botanical language: Cryptogamae, including Thallophyta (algae and fungi), Bryophyta (mosses and liverworts), and Pteridophyta (ferns and fern allies), and Phanerogamae, including Gymnospermae and Angiospermae. From an evolutionary perspective, the Thallophyta were regarded as more primitive than the Bryophyta, these more primitive than the Pteridophyta, and so on.

Based on the Eichler system, a new, detailed, phyletic system of classification was produced also in Germany by Heinrich Gustav Adolf Engler (1844–1930) and his associate, Karl Anton Eugen Prantl (1849–1893). Engler was professor of botany at the University of Berlin and director of the Berlin Botanical Garden from 1889 to 1921. Their new phyletic system was first published by Engler in outline form in 1886 as a guide to the Breslau botanical garden and more fully in their 23-volume work, *Die natürlichen Pflanzenfamilien* (1887–1915), which was essentially a world flora at the generic level (a new *Genera Plantarum*).[1] Many of the groupings in the classification were derived from the natural system of Bentham and Hooker. The conspicuous difference was that very definite ideas were advanced as to which groups of plants were most primitive and which were more derived. Within the flowering plants, those families with unisexual flowers borne in catkins (or aments), called the Amentiferae, were judged most primitive on the basis of their presumed resemblance to gymnospermous ancestors. Many lines of descent from that basic complex were elaborated. The most important point is that this was a system in which evolutionary interpretations of relationships among groups abounded.[2] This was, and still is, the dominant feature of the phyletic approach to classification.

Charles Edwin Bessey (1845–1915), a student at Harvard for six months under Asa Gray, worked most of his career at the University of Nebraska and produced a phyletic system of classification (1915), the concepts of which are still basically followed today. As Cronquist aptly remarked: "We are all, or nearly all, Besseyans" (1968:52). Bessey departed from the ideas of Engler and instead of viewing the Amentiferae as most primitive, he regarded the Polycarpicae or Ranales as the most primitive group with many separate, helically arranged, floral parts with bisexual flowers.

Many additional new phyletic systems of classification for the angiosperms have been published since Bessey's time (table 5.1). These include the systems of Hutchinson (1926, 1934, 1969); Cronquist (1968, 1981, 1983, 1988); Thorne (1968, 1976, 1983, 1992a, 2000a, b); Takhtajan (1969, 1980, 1986, 1987, 1997); Stebbins (1974); R. Dahlgren (1975, 1980, 1983); Goldberg (1986); and G. Dahlgren (1989a, b). It is not my purpose here to review these systems in detail, but only to stress that all of them are phyletic in the sense of emphasizing primitive vs. derived character states and groups and drawing lines of descent between and among taxa. (See Lawrence 1951 and Core 1955 for presentations and discussion of many of the older systems, plus the additional works cited above for the most recent contributions; see also tabular comparisons of some of these systems in Becker 1973 and Swift 1974; good summaries are also provided in Brummitt 1992.)

It is important to stress, however, that the most recent comprehensive classification of angiosperms is no longer intuitively phyletic, but rather explicitly cladistic: that deriving from the Angiosperm Phylogeny Group (APG 1998 and APG II 2003). The rise of cladistic methods of classification (outlined in Chapter 8), combined since the 1990s with new DNA sequence data (especially *rbcL*; Chase et al. 1993), has now yielded a new classification of angiosperm families and orders. Whereas phenetics never resulted in a new, accepted, comprehensive classification of the angiosperms, cladistics

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[1] The impact of this publication was so great that the arrangement of most of the world's herbaria is still based on this scheme (including our collection in Vienna, Austria), even though more modern phyletic systems of classification exist. None of the more modern systems are so detailed, so well indexed, and so well numerically coded to genus and family, all of which have aided the permanence of the Engler system as useful for storage and retrieval of specimens. Updated editions have also been published regularly (e.g., Melchior 1964).

[2] Turrill mentioned that "Engler did not consider his system as phylogenetic, in the complete sense of the word, but rather as one in which the groups are built up in a step-like manner to form, as far as possible, a generally progressional morphological series. Some of the groups are acknowledged to be probably polyphyletic" (1942:268). It was, nonetheless, phyletic in the context used here in contrast to the pre-Darwinian natural systems.

now has. The closest we came with phenetics was the valiant effort for dicotyledons by Young and Watson (1970). The APG classifications are important for two reasons: (1) they represent the first comprehensive classification of the angiosperms (the dominant vegetation on earth) done quantitatively; and (2) they were done by a consortium of more than two dozen workers, not by a lone expert (most unusual, as stressed by Endersby 2001). The impact of these classifications has been enormous; they now provide the basis for new textbooks of systematic botany (Judd et al. 2002; Spichiger et al. 2004; Simpson 2006); a new, major, general synthesis on angiosperm phylogeny and evolution (Soltis et al. 2005); and even identification and overview manuals (Souza and Lorenzi 2005; Spears 2006; Heywood et al. 2007). A new system of classification of genera and families of flowering plants is now in progress under the general editorship of K. Kubitzki (vols. 1–8 already published; Kramer and Green 1990; Kubitzki, Rohwer, and Bittrich 1993; Kubitzki 1998a, b, 2004; Kubitzki and Bayer 2003; Kadereit 2004; Kadereit and Jeffrey 2007). The later volumes strongly rely on the new molecular data. This experience makes clear that any future improvement in broad classification of the angiosperms will no doubt be based on molecular data (e.g., Chase, Fay, and Savolainen 2000) in the context of quantitative analyses (cladistic and/or phenetic) and involving many persons. This is a fundamental change in plant systematics. It does not necessarily mean that we will see cladistics replacing phyletics in general plant classification, however, because the latter can also be done quantitatively with molecular data (more on this in Chapter 9).

Because development of any intuitive classification involves a subjective selection of characters and resulting subjective comparison and evaluation of character states, legitimate differences have arisen among taxonomists even when examining the same set of organisms. Some workers will stress certain kinds of characters, and some will emphasize others. Even when admitting the same discontinuities in the data, some might evaluate these gaps in terms of a larger difference in ranking than would others. For example, one might believe the observed discontinuity to indicate hierarchical difference at the generic level, whereas another might prefer to recognize the difference only at the specific level. Among practicing taxonomists, therefore, acceptable differences of opinion regarding certain groups occur. When these viewpoints are applied to large numbers of different organisms, the resulting classifications can be very divergent in regard to the number of units recognized at each hierarchical level. Workers who tend to take a broader view of grouping and ranking have been nicknamed "lumpers," and those with the opposite viewpoint are called "splitters" (e.g., McKusick 1969). Splitters tend to believe that morphological variations of a "minor" nature should be documented formally by the description of new taxa, whereas lumpers may observe the same variations but believe that their formal recognition is neither necessary nor desirable. It is important to emphasize that both these approaches to classification are legitimate and acceptable, within limits, even though through the years such differences of opinion have been the sources for heated (and sometimes personal) debates among the persons involved. Excessive splitting and lumping are to be avoided. Generally speaking, there tends to be less difference in viewpoint as more different types of data and more complete data are used.

Definitions of "Naturalness"

The definition of natural classification used in this book is not shared by all workers, and therefore, a brief discussion of this point is in order. This is important before we consider phenetic and cladistic approaches to classification because some practitioners of each have called their efforts and results "natural." Pre-Linnaean workers sometimes used natural classification in the sense of determining the true "nature" or "essence" of plants, an idea derived from Plato and supported by belief in Special Creation (Davis and Heywood 1963). Post-Linnaean (but pre-Darwinian) systems used natural in the sense of Jussieu's system, i.e., a classification based upon overall similarity (e.g., Lindley 1830a, b). The usage up to this point was clear enough; the problems of interpretation developed after evolutionary thinking and phyletic approaches to classification appeared.

Darwin (1859, p. 323) made very clear his meaning of "natural" in reference to systems of classification:

> The Natural System is founded on descent with modification; that 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, and, in so far, all true classification being genealogical; that community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation, or the enunciation of general propositions, and the mere putting together and separating objects more or less alike. But I must explain my meaning more fully. I believe that the *arrangement* of the groups within each class, in due subordination and relation to other groups, must be strictly genealogical in order to be natural; but that the *amount* of difference in the several branches or groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different genera, families, sections, or orders (1859:420).

It is clear, therefore, that Darwin rejected essentialism and also the naturalist's overall similarity (such as Jussieu's) in favor of an emphasis on genealogical relationship and character divergence within lineages as the bases for natural classification. Padian (1999) went to great lengths to argue that Darwin advocated only genealogy as the basis for classification, but I remain unconvinced, preferring to follow Mayr (1982). The issue is admittedly historically complex.

Gilmour's use of "natural" has been quoted and discussed by many workers (e.g., Heywood 1989). He stresses: "A natural classification is that grouping which endeavours to utilize *all* the attributes of the individuals under consideration, and is hence useful for a very wide range of purposes. . . . Phylogeny, therefore, instead of providing the basis for the one, ideal natural classification, is seen to take its place among the other subsidiary classifications constructed for the purpose of special investigations. It may also be regarded as forming a sort of background to a natural classification, since, although natural groups are not primarily phylogenetic, they must, in most cases, be composed of closely related lineages" (1940:472, 473). For his earlier, but consistent, views of 1936 and 1937, see Gilmour (1989). Davis and Heywood agreed with this perspective: "We do not suggest ignoring phylogenetic facts. It is the basing of classification on inferred phylogeny, instead of interpreting classification in phylogenetic terms, to which we are opposed" (1963:68).

The pheneticists (e.g., Sokal and Sneath 1963; Sneath and Sokal 1973), agreed with Gilmour's definition of naturalness and used this as their philosophical underpinning for seeking many (upwards of 100) characters to produce phenetic classifications. Despite Gilmour's use of "*all* the attributes," cited above, he clearly did not mean the extremely large number of characters advocated by pheneticists. From reading his general paper, one sees clearly that his natural classification "in practice, is the procedure followed in what is sometimes called 'orthodox' taxonomy, and it would seem best to confine the use of the ordinary taxonomic categories of species, genus, family, &c., to a natural classification of this type. In so far as it is theoretically possible to envisage a classification on these lines, which does in fact embody all the attributes of the individuals being classified, it can be said that one final and ideal classification of living things is a goal to be aimed at. In practice, however, this aim would never be attained, owing both to the limitations of our knowledge and to the differences of opinion between taxonomists" (1940:472). Gilmour's main stress, therefore, is that all correlating characters of whatever type from whichever parts of the organism should be used to produce a natural classification. This is natural in the same sense as with pre-Darwinian authors and provides no new philosophical base for phenetic practitioners.

Cladistic advocates have equated natural with their use of the term "phylogenetic," or in the context of this book, the "cladistic," relationship. Wiley spoke of "phylogenetic naturalness" in which "the members of a phylogenetically natural group share a common ancestor not ancestral to any other group" (1981a:71). This formed a part of Darwin's concept of naturalness and was essentially the same as that used by Mayr (1969c:78). Wiley continued, however, with a definition of "a natural taxon" as "a taxon that exists in nature independent of man's ability to perceive it" (p. 72). This is a different and much more general usage of "natural."

CHAPTER

7

The Phenetic Approach

Not all taxonomists, however, have found the phyletic approach to classification satisfactory. Some workers, especially in the early 1960s (e.g., Sokal and Sneath 1963; Sneath and Sokal 1973) regarded this method as too subjective, and as evidence they pointed to different classifications generated by different taxonomists for the same sets of organisms. They gave striking examples of lumping vs. splitting in intuitive phyletic classification, especially in groups that are strongly inbreeding or with asexual nodes of reproduction (e.g., in *Crataegus* and *Taraxacum*). In these cases, widely divergent views have prevailed even with examination of more or less the same collections and other available evidence. The subjectivity of the intuitive phyletic approach is evident in the selection of different characters to be compared, the comparison of character states, and the ranking of the resultant groups. Attempts have been made, therefore, to avoid (or at least reduce) this subjectivity, particularly in the process of grouping, by: (1) emphasizing the selection of as many characters as possible (ideally *all* the characters, harking back to the "naturalness" of Gilmour 1940); (2) making the description and measurement of character states as precise as possible; and (3) comparing the character states of the individuals by rigidly defined numerical procedures.

Definitions

These perspectives have led to the development of the phenetic approach to classification. *Phenetics* is here defined as a method of classification based on numerous precisely delimited characters (with carefully coded states) usually of equal weight and their comparison by an explicit method of grouping. The term *phenetic* was introduced by Cain and Harrison to mean a relationship "by overall similarity, based on all available characters without any weighting" (1960:3). Sokal and Sneath used phenetic to refer to a relationship between taxa "evaluated purely on the basis of the resemblances existing *now* in the material at hand" (1963:55) and "the overall similarity as judged by the characters of the organisms without any implication as to their relationship by ancestry" (p. 3). This was redefined to read: "similarity (resemblance) based on a set of phenotypic characteristics of the objects or organisms under study" (Sneath and Sokal 1973:29). Burtt questioned whether equal weighting should be regarded as a necessary part of phenetics and suggested the term *isocratic* for characters with "equal power" (1964:15). Colless (1971) commented that weighted characters based on "conservative" patterns of variation in populations (Farris 1966) could indeed be used in determining phenetic relationships, and Adams (1975a) showed how this could be done in classifying species of *Juniperus*. Moss advocated treating phenetics as

> the estimation of relationship due to similarity, but effectively becoming *independent of data base treatment*. Such an interpretation emphasizes that phenetic relationships are similarity relationships obtained when comparing the phenotypes of organisms (or objects) for correspondences of parts; conversely, such relationships are phenetic, regardless of whether the relative weights of characters used to describe these parts are: 1) left unmodified as raw data, with possible unintentional weighting of some characters due to scale factors, 2) equalized due to a process such as standardization by range or variance, or 3) variously modified as the result of logically or biologically valid or invalid assumptions made by the investigator. (1972:237)

Equal weighting is explicit in the definition of phenetics used here, because employment of many differentially weighted characters would be regarded as a complex attempt at natural or phyletic classification.

Numerical taxonomy was coined by Sokal and Sneath as "the numerical evaluation of the affinity or similarity between taxonomic units and the ordering of these units into taxa on the basis of their affinities" (1963:48). Later they offered a slightly different definition: "the grouping by numerical methods of taxonomic units into taxa on the basis of their character states" (Sneath and Sokal 1973:4). The intent was that methods of numerical taxonomy would be used to determine phenetic relationships among organisms, and this has been the usual approach. In the minds of some workers, however, numerical taxonomy means simply the use of some quantitative assessment of relationships in classification, usually with help of the computer (Duncan and Baum 1981).[1] This broader context has also been labelled *statistical systematics* (Solbrig 1970b:178) or obvious similar appellations, such as *statistical taxonomy*, *mathematical taxonomy*, or *quantitative taxonomy*. Hence, some prefer the term *numerical phenetics* (Duncan and Baum 1981) for studies employing equal weighting of characters. Other terms in use have been *taximetrics* (Rogers 1963), *taxometrics* (Mayr 1966),[2] and *multivariate morphometrics* (Blackith and Reyment 1971).

Morphometrics is now regarded as distinct from phenetics, and a few comments on this point are in order. *Morphometrics* can be defined as the determination of relationships based on continuous characters, especially linear measurements (Jensen 2003). This is not necessarily the same as phenetics, which can utilize qualitative as well as quantitative data in an unweighted context. Morphometrics derived from the methods used in phenetics, but the former focuses on understanding complex morphological relationships among taxa primarily at the lower levels of the taxonomic hierarchy and is interested in fundamental questions of the evolution of shape. This has become, then, primarily a tool to understand population-level phenomena. A definitional complication, however, has entered the picture due to influences from cladistics (see Chapter 8). The origin of cladistics was partly due to a reaction against phenetics, whereby it was believed desirable to return phylogenetic concepts back into classification. So strong were the criticisms against phenetics by cladists that some pheneticists abandoned the term altogether, preferring to substitute morphometrics. Because morphometrics has now developed clearly into a field of its own (e.g., Rohlf and Bookstein 1990; Bookstein 1991; Marcus et al. 1996), this term is *not* used as a synonym of phenetics in this book. Things keep changing so much, in fact, that some workers are now seeking phylogenetic signals in morphometric data (Wiens 2000).

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[1] An amusing twist is found in the paper by P. J. H. King (1976) on "taxonomy of computer science," in which organisms (people) are classifying computers and activities associated with them rather than the reverse.

[2] Mayr (1966) preferred "taxometrics" instead of "taximetrics" because it "is a word in a modern language and formed in analogy to taxonomy" (p. 88) and also, tongue-in-cheek, because "The word taximetrics has the additional disadvantage, as a mischievous friend of mine reminded me, that the name suggests 'the science of taxi meters.'" See also Heywood and McNeill (1964a) and Pasteur (1976) for discussions of these and related terms.

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Taxon Index

Subject Index

Numbers in **boldface** indicate definitions of terms when more than one page is given; those in *italics* refer to major discussions.