

(Second Edition)

植物系统学

(原著第二版)

Michael G. Simpson









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生命科学新经典

Plant Systematics

(Second Edition)

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What is meant by the natural system; it is genealogical in its attempted arrangement, with the grade of acquired difference marked by the terms varieties, species, genera, families, orders, and classes—Darwin (1859)

On the Origin of Species by Means of Natural Selection

从 38 亿年前至今,地球上的生命有机体经历了一个漫长的进化过程,形成了丰富多样和绚丽斑斓的生物世界。面对充满好奇的各类生物,人们把最相似的个体归在一起并命名,而与其他不同的归类进行区别。可以想象,这种分类学思想的萌芽应该在人类认识自然界的最初阶段就出现了。中国古代早在殷商时期(公元前 1600~1066 年)就开始用甲骨文记录植物名称,在公元前约 600 年的《诗经》中就提到黍、韭、榛、桑等 130 多种植物,并出现"灌木"和"乔木"等名称。在西方,古希腊人亚里士多德(Aristotle,公元前384~322 年)被认为是分类学之父,他利用比较的方法把 580 种动物按照其具有的独特性状和共同特征进行了归类,分成鸟类(birds)、鱼类(fishes)等。亚里士多德也对植物进行了分类,可惜著作遗失,他的学生西奥弗拉斯脱斯(Eresio Theophrastos,公元前 371~286年)在其《植物的历史和植物本原》(De Historia et De Causis Plantarum)一书中记载了 500 多种植物。尽管当时他未建立正式的分类系统,但提出了一些分类标准,把植物分成乔木、灌木、草本等。因此,西奥弗拉斯脱斯在欧美的不少教科书中被认为是植物分类学的奠基人。

系统学(systematics)一词在文献或书籍中的出现始于林奈(Carl Linnaeus, 1707~1778)(Linnaeus, C., 1753,Species Plantarum, 2 vols, Stockholm)。随后,在 Smith(An Introduction to Physiological and Systematical Botany, 1809)和 Nuttall(An Introduction to Systematic and Physiological Botany, 1827)等人的著作中,系统植物学(Systematic Botany)作为一门学科被提了出来。系统学最初的含义是将命名的生物按照某个鉴别性状或顺序排列起来。林奈时期的学者认为:尽管在种内存在变异,但种是上帝创造的,因而是固定不变的,并强调通过研究形态特征,根据物种的相似或不同将其排列到一个系统中去,来反映神圣的造物主的意旨(Divine Plan)。在此期间,系统学(systematics)和分类学(taxonomy)被认为是同义词。

1859 年,达尔文(Charles Darwin,1809~1882)的《物种起源》巨著问世,其生物进化理论对于系统学研究产生了深刻影响。系统学家的兴趣不再限于对物种进行描述和分门别类,而且试图理解分类群的系统发育和进化关系,更有一部分系统学家对于进化过程本身,即生物多样性产生的机制感兴趣。从达尔文时代开始,系统学和分类学有了不同的含义,前者逐渐扩大其研究范围,除了包括分类学之外,还充分利用来自于生物学其他分支学科,如胚胎学、细胞学、遗传学、分子生物学、发育生物学、基因组学等的实验技术、最新成果和证据,探讨生物群的系统发育和进化。由于系统学的研究内容越来越多样庞杂,因此任何具体的描述均不能够准确地定义这一学科,为了避免争论,美国著名系统与进化生物学家 Ernst Mayr 选择最简单明了的方式,把系统学定义为"研究生物多样性的科学"。

综上所述,系统学具有两个突出的特点: (1) 它是一门古老的学科,即使从林奈时期算起,至少也有250年的历史; (2) 它是一门无穷综合的学科,要求不断追踪生命科学研究的前沿。正是这两大特点,浩繁的文献积累给系统学的初学者带来极大负担。该书作者充分考虑到初学者的困难,一方面对传统方法和经典内容进行了全面讲解,包括第三、四部分,四个附录和术语解释部分。在介绍这些内容时,既注重系统性,使初学者易于掌握,又体现出实用性,使初学者在实际工作中方便使用。在第9章,作者结合类群,图文并茂,对各类形态学术语的解释详尽,且清楚易懂,即使在一些收词较全的术语词典中亦难查到如此细微准确的释义,实为该书的一大特色。例如对藤本习性的描述,作者

比较了 clambering(scandent,攀援但无特殊附着结构)和 climbing(攀援但有卷须、叶柄、不定根等附着结构),以及 prostrate(匍匐但节上无根)、repent(匍匐但节上有根)、decumbent(匍匐上行)等词的用法,读完这段内容,再参考图 9.4,读者可以把之前从文献上看到的这些术语系统起来,通过对比便能更加正确地用它们进行描述。再如,对 connate(同类结构合生、不易分离,如雄蕊与雄蕊),adnate(不同类结构合生、不易分离,如雄蕊与花瓣),coherent(同类结构部分或不完全合生、易分离),adherent(不同类结构部分或不完全合生、易分离),distinct(同类结构离生),free(不同类结构离生),contiguous(靠合)这组在实际描述中容易用错的词汇集中在一起讲解,则非常易懂而不再混淆。在第 10~13 章,作者对在系统学上有进化意义的性状的解释是能详则详,深入浅出,如导管、筛管类型,胚囊类型和发生发育过程,花粉外壁超微结构和萌发孔类型等。在术语解释部分,与同类教科书相比不仅收录的词汇多,而且释义清楚易懂。

另一方面,该书作者通过阅读大量文献,尽可能地反映植物系统学领域的最新进展。在第6~8章 介绍被子植物系统时,在2006年第1版中采用APG II系统,时隔4年之后在第2版的修订中则采用了APG III系统,对大多数类群的定义参考了分子系统学研究的结果,强调其单系性。在整个第二部分,从绿色植物到陆地植物(有胚植物或高等植物),再到维管植物、种子植物和有花植物,在讲解从低等类群向其高一级的类群进化时,将关键创新性状贯彻始终,并加以强调,就使得读者容易理解植物界的多样性以及进化的脉络与线索。

从系统学产生以来,系统学家在立题时习惯于选择一个分类群开展工作,即首先关注的是该类群是否还有分类学问题尚待解决,至于所选择的类群是否具有一般性的或意义重大的科学问题则放到次要的位置,这与大多数实验生物学家在选题时首先关注科学问题几乎是完全相反的思路。然而,系统学发展到今天,特别是与分子遗传学、发育生物学、生态学和信息科学的结合,已成为生命科学领域的研究热点,随着各个类群的分类学问题及分类群之间的关系越来越清楚,一些进化问题被提出来,这使得系统学家的选题思路发生了变化,即首先提出科学问题,然后再选择适合的类群设计实验开展工作。该书在这方面给研究者提供了一个起点,尤其是刚刚加入到该领域的年轻学者可以比较快地对以往几百年来分类学和系统学的发展历史以及最近同行们所关注的问题和取得的进展有一个全面的框架性的了解,从而能够更加准确地选题。为此,作者在前言的最后建议系统学研究者在开展工作之前一定要清楚其研究的目的,即首先了解为什么要选择做这项工作(Why it is that we do what we do)。

总之, 这是一部理论性和实用性很强的教科书, 特别向植物系统学及其相关专业的读者推荐。

陈之端 路安民 中国科学院植物研究所 2011年10月10日

前 言

《植物系统学》是一本关于陆地植物形态、分类和进化的人门教科书。书中介绍了植物系统学的基本原理和方法、研究目的、证据来源和术语,总结了关于对植物类群进化关系的最新理解和该领域至关重要的实用信息。我努力将这些知识和信息以精简和清晰的方式展示给初学者,以便他们能够较好地理解和掌握该领域浩繁信息中较为重要的部分,继而从文献中进一步扩充更多细节。

本书适用于研究生或高年级本科生的植物系统学或分类学课程学习,其中的一些内容亦可用于植物区系学、植物形态学、植物多样性或普通植物学课程的教学。

此书有一个很实用的特点,就是在每一章的首页都有一个详细的目录列表。这个做法是由我的学生们建议的。大量线条图和彩色照片贯穿于本书的各章节,其中用被解剖或标注的植物图片来展示重要检索或识别特征,是本书的另一特点。每一章的最后都附有(1)用于巩固章节内容的复习题;(2)供学生练习和实践的材料;(3)文献部分列举了一些基础的和最近的文献用以拓展学习。但这并不全面,因而鼓励学生们根据自己的研究兴趣作进一步的文献搜索(见附件3),在一些章节中还有网址列举。

全书内容由五个部分组成,每部分包括一至若干章。当然,教师可以根据个人喜好和关注类群改变这些部分或者各部分内的章节顺序。在不同部分中某些章节的内容有少量重复,用以保持其独立性。

第一部分(系统学)对植物系统学的概念和方法进行了概述。第1章介绍了植物的科学定义、关系、分类和重要性,并总结了系统学、分类学、进化和系统发育学的基本概念和原理。第2章详细介绍了系统发育系统学以及推导系统发育树或分支图的理论和方法,包括简约法、贝叶斯法和最大似然法。

第二部分(植物的进化和多样性)详细描述了植物的性状和分类。我希望初学者通过对本部分的学习能够基本上理解绿色植物和陆地植物(第3章)、维管植物(第4章)、木本植物和种子植物(第5章)和有花植物(第6~8章)的进化。第3~5的每章均包括两个主要方面:一是利用分支图(系统发育树)来展示类群的进化历史,同时在分支图上标注每一个重要的衍生进化特征,即衍征或近裔特征(apomorphies),以此来强调这些特征可能的适应意义。利用这种方法学习大类群及其衍征比单纯记忆一长串特征要容易些。把这些衍征看作是独特进化事件的产物,尤其是当它们在功能上潜在的意义被理解之后,这些衍征就变得"生动"起来。另一方面,在第2版中,我对有争议类群的多样性进行了探讨,增加了一些科的详细描述,包括石松类(全部3个科),蕨类(37科中的15科)和裸子植物(13科中的9科)。基于模式属名称对科名的语源进行了追溯,同时用方括号附注了少数特例和异名。对大类群中的代表性植物进行描述和图释,以便学生们能够理解和识别这些植物主要谱系的基本特征。

对于有花植物,亦即被子植物来说,因其丰富的多样性而用三大章来阐述。第6章讨论了有花植物的进化,对其近裔特征(衍征)作了细致描述,对有花植物起源作了概括性介绍。第7和第8章对有花植物的具体类群进行了描述。第7章是非真双子叶类,包括被子植物的早期分化类群和单子叶植物,第8章是真双子叶植物,包括了大多数被子植物。在这两章中对被子植物约400科中的129科进行了详细的描述,并配有照片和绘图;这些科大多数是常见的类群且实验材料容易采集获得。另外一些科用一个或多个代表植物进行了例举,但未描述。我尽力去强调各科的鉴别特征以便学生们识别,并增加了列举科内类群的一些重要经济用途。专业术语请参见第9章和第10~14章的部分内容(或术语解释部分)。除个别例外,本书被子植物分类系统采用 APG III 系统,该系统以目为主要分类阶元,把关系相近的科归于同一目中,事实证明此系统用于展示有花植物丰富的多样性是非常适用的。

第三部分(系统学证据与描述性术语)从植物形态学一章(第9章)开始。注释文字以及丰富的模式线条图和照片有助于训练初学者能够准确且全面地描述植物的形态。附录1和2(见本书最后部分)应与第9章配合使用。本部分的其他章包括了植物解剖学(第10章)、植物胚胎学(第11章)、孢粉学(第12章)、植物生殖生物学(第13章)和植物分子系统学(第14章)方面的基本描述性术语。在一本植物系统学的教科书中包括上述内容的合理性在于来自这些涉及不同领域的术语在系统学研究、系统发育重建和分类处理时常常被用到。尤其是在最后一章植物分子系统学中综述了该学科的基本技术手段和获取的数据类型,这些数据反映了植物系统学家们最近几年内在分子系统发育重建研究中所取得的丰硕成果。

第四部分(植物系统学信息资源)讨论了在日常系统学研究中一些根本的、也是必不可少的方面。植物的鉴定一章(第15章)对比分析了常规的二歧检索和智能化多路径检索,并概括了一些实用鉴定方法。植物的命名一章(第16章)总结了最新国际植物命名法规的基本规则,包括有效发表新种的步骤和植物学拉丁名称概述。在植物的采集和记录一章(第17章)着重阐述了植物采集和数据获取的正确方法,数据获取在当前的生物多样性与保护生物学研究中显得尤为重要。最后,标本馆和数据信息系统一章(第18章)介绍了标本馆管理流程和技术,并且强调了计算机数据库系统在植物采集中分析以及整合形态、生态和生物地理数据中发挥的作用。

第五部分(物种概念和保护生物学)是第二版中新加的内容,仅有一章(第19章)。该章简述了植物的生殖、物种标准和概念及种下分类。此外,在保护生物学部分,概括地介绍了该领域的基本概念,保护生物学与分类学和系统学的关系以及对生物学家和社会的重要意义。

最后,是四个附录和一个术语解释部分。以我个人之见,这些部分在我的植物系统学课程中颇有价值。附录 1 是用于详细描述植物的性状清单(见植物系统学信息资源网站),这个清单能够训练学生写出达到发表水平的物种描述。附录 2 对植物学绘图作了简要讨论。我认为学生们很有必要学习植物学绘图以培养他们的观察技能。附录 3 列举了植物系统学领域中的学术期刊并附有训练查找文献能力的练习题。附录 4 也是第二版新增内容,它简述了统计学和形态计量学以及如何利用这些方法解决分类学和系统发育系统学问题。在术语解释部分,对本书中出现的所有术语给出它们的定义,并指出其同义词、形容词形式、复数形式、缩写和类比术语。

三个网站与本书关联: (1) 植物系统信息资源网(http://www.sci.sdsu.edu/plants/plantsystematics) 具有网络连接和普遍获取的材料; (2) 随书发行网站(http://www.elsevierdirect.com/companions/9780123743800),可下载本书各章的图谱,附录材料以及本书作者主页链接; (3) 教学资源网(http://textbooks.elsevier.com/web/login.aspx),资料需要授权登录获取,请用 textbooks@elsevier.com 与销售代理商联系。

贯穿本书的始终,我试图坚持用 W-H-Y 即 What-How-Why 去组织和阐述各章内容。(1)它是什么,主题是什么,基本定义是什么?(很多科学上的问题争论,如果有一个清楚的表述或专业定义很可能在一开始就可以被解决掉。)(2)怎样去解决问题?材料和方法是什么,获取数据的技术手段有哪些,分析数据的类型是什么?(3)为什么要这样做?目的、宗旨或目标是什么,核心的范式是什么?目前的研究或关心的问题与其他哪些方面有关联?这个简单的 W-H-Y 方法最早是由我的好友兼导师,A. E. Radford 教授传授给我的,无疑对于任何一项科研探索都是有益的,是任何老师教导学生不可疏忽的一个环节,如此不仅能锻炼他们的写作技能,而且还有助于他们批判性地审视科学问题。

最后,我建议老师和学生中的任何人,都应该时不时地静下来思考我们目前所做的事情的目的和意义是什么。数年来,我提炼了自己的见解,并且建议将以下三个方面作为从事科研的可能目标: (1)去感知和探索大自然的美丽、博大以及千丝万缕的联系; (2)尽情去享受科学发现的激动和快乐; (3)体味和分享学习的乐趣。正是在这种精神的感召下,我真诚地希望这本教科书能对他人有用。

The first edition of this book was dedicated to three mentors I have been very fortunate to know: Albert Radford, who taught critical thinking; P. Barry Tomlinson, who taught the fine art of careful observation; and Rolf Dahlgren, whose magnetic personality was inspirational. I also wish to thank my many students who have provided useful suggestions over the years, plus three writers who captured my interest in science and the wonder of it all: Isaac Asimov, Richard Feynman, and Carl Sagan.

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

PREFACE

Plant Systematics is an introduction to the morphology, evolution, and classification of land plants. My objective is to present a foundation of the approach, methods, research goals, evidence, and terminology of plant systematics and to summarize information on the most recent knowledge of evolutionary relationships of plants as well as practical information vital to the field. I have tried to present the material in a condensed, clear manner, such that the beginning student can better digest the more important parts of the voluminous information in the field and acquire more detailed information from the literature.

The book is meant to serve students at the college graduate and upper undergraduate levels in plant systematics or taxonomy courses, although portions of the book may be used in flora courses and much of the book could be used in courses in plant morphology, diversity, or general botany.

Each chapter has an expanded Table of Contents on the first page, a feature my students recommended as very useful. Numerous line drawings and color photographs are used throughout. A key feature is that illustrated plant material is often dissected and labeled to show important diagnostic features. At the end of each chapter are (1) Review Questions, which go over the chapter material; (2) Exercises, whereby a student may apply the material; and (3) References for Further Study, listing some of the basic and recent references. Literature cited in the references is not exhaustive, so the student is encouraged to do literature searches on his/her own (see Appendix 3). Web sites are listed for some chapters.

The book is classified into units, which consist of one or more chapters. Of course, a given instructor may choose to vary the sequence of these units or the chapters within, depending on personal preference and the availability of plant material. There is a slight amount of repetition between chapters of different units, but this was done so that chapters could be used independently of one another.

Unit 1, Systematics, gives a general overview of the concepts and methods of the field. Chapter 1 serves as an introduction to the definition, relationships, classification, and importance of plants and summarizes the basic concepts and principles of systematics, taxonomy, evolution, and phylogeny. Chapter 2 covers the details of phylogenetic systematics, and the theory and methodology for inferring phylogenetic trees or cladograms, including parsimony, Bayesian, and maximum likelihood methods.

Unit 2, Evolution and Diversity of Plants, describes in detail the characteristics and classification of plants. The six chapters of this unit are intended to give the beginning student a basic understanding of the evolution of Green and Land Plants (Chapter 3), Vascular Plants (Chapter 4), Woody and Seed Plants (Chapter 5), and Flowering Plants (Chapters 6–8). Chapters 3–5 are formatted into two major sections. The first section presents cladograms (phylogenetic trees), which portray the evolutionary history of the group. Each of the major derived evolutionary features (apomorphies) from that cladogram is described and illustrated, with emphasis on its possible adaptive significance. This evolutionary approach to plant systematics makes learning the major plant groups and their features conceptually easier than simply memorizing a static list of characteristics. Treating these features as the products of unique evolutionary events brings them "to life," especially when their possible functional significance is pondered. The second section of Chapters 3-5 presents a survey of the diversity of the group in question. New to this second edition are detailed family descriptions of lycophytes (all 3 families treated), ferns (15 of 37 families treated), and gymnosperms (9 of 13 families treated). Family etymologies are included, these, of course, based upon the type genus name; rare conditions and synonyms are enclosed by square brackets. Exemplars within major groups are described and illustrated, such that the student may learn to recognize and know the basic features of the major lineages of plants.

Because they constitute the great majority of plants, the flowering plants, or angiosperms, are covered in three chapters. Chapter 6 deals with the evolution of flowering plants, describing the apomorphies for that group and presenting a synopsis of their origin. Chapters 7 and 8 describe specific groups of flowering plants. In Chapter 7 the non-eudicot groups are treated, including the earliest diverging angiosperm lineages and the monocotyledons. Chapter 8 covers the eudicots, which make up the great majority of angiosperms. In these two chapters numerous flowering plant families (129 of ca. 400 recognized) are described in detail, accompanied by photographs and illustrations; these are mostly families that are commonly encountered or for which material is usually available to the beginning student. Additional families are not described, but are illustrated with one or more exemplars. I have tried to emphasize diagnostic features a student might use to recognize a plant family, and

have included some economically important uses of family members. Reference to Chapter 9 and occasionally to Chapters 10–14 (or use of the comprehensive Glossary) may be needed with regard to the technical terms. The Angiosperm Phylogeny Group III system of classification is used throughout (with few exceptions). This system uses orders as the major taxonomic rank in grouping families of close relationship and has proven extremely useful in dealing with the tremendous diversity of the flowering plants.

Unit 3, Systematic Evidence and Descriptive Terminology, begins with a chapter on plant morphology (Chapter 9). Explanatory text, numerous diagrammatic illustrations, and photographs are used to train beginning students to precisely and thoroughly describe a plant morphologically. Appendices 1 and 2 (see below) are designed to be used along with Chapter 9. The other chapters in this unit cover the basic descriptive terminology of plant anatomy (Chapter 10), plant embryology (Chapter 11), palynology (Chapter 12), plant reproductive biology (Chapter 13), and plant molecular systematics (Chapter 14). The rationale for including these in a textbook on plant systematics is that features from these various fields are described in systematic research and are commonly utilized in phylogenetic reconstruction and taxonomic delimitation. In particular, the last chapter on plant molecular systematics reviews the basic techniques and the types of data acquired in what has perhaps become in recent years the most fruitful of endeavors in phylogenetic reconstruction.

Unit 4, Resources in Plant Systematics, discusses some basics that are essential in everyday systematic research. Plant identification (Chapter 15) contains a summary of both standard dichotomous keys and computerized polythetic keys and reviews practical identification methods. The chapter on nomenclature (Chapter 16) summarizes the basic rules of the most recent International Code of Botanical Nomenclature, including the steps needed in the valid publication of a new species and a review of botanical names. A chapter on plant collecting and documentation (Chapter 17) emphasizes both correct techniques for collecting plants and thorough data acquisition, the latter of which has become increasingly important today in biodiversity studies and conservation biology. Finally, the chapter on herbaria and data information systems (Chapter 18) reviews the basics of herbarium management, emphasizing the role of computerized database systems in plant collections for analyzing and synthesizing morphological, ecological, and biogeographic data.

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

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

Lastly, four Appendices and a Glossary are included. I have personally found each of these addenda to be of value in my own plant systematics courses. Appendix 1 is a list of characters used for detailed plant descriptions (available on the Plant Systematics Resources web site). This list is useful in training students to write descriptions suitable for publication. Appendix 2 is a brief discussion of botanical illustration. I feel that students need to learn to draw in order to develop their observational skills. Appendix 3 is a listing of scientific journals in plant systematics, with literature exercises. Appendix 4, new to the second edition, gives a brief overview of statistical and morphometric methods and how those may be applied in addressing questions in taxonomy and phylogenetic systematics. The Glossary defines all terms used in the book and indicates synonyms, adjectival forms, plurals, abbreviations, and terms to compare.

Three web sites will be available to be used in conjunction with the textbook: (1) a Plant Systematics Resources site (http://www.sci.sdsu.edu/plants/plantsystematics), with web links and materials that are universally available; (2) a companion website (http://www.elsevierdirect.com/companions/9780123743800) that includes the chapter figures, appendix material from the textbook, and links to the author's website; and (3) an Instructor Resources site (http://textbooks.elsevier.com/web/Login.aspx), with material that is password protected. Please contact your sales representative at textbooks@elsevier.com for access to the Instructor Resources site.

Throughout the book, I have attempted to adhere to W-H-Y, What-How-Why, in organizing and clarifying chapter topics: (1) What is it? What is the topic, the basic definition? (Many scientific arguments could have been resolved at the start by a clear statement or definition of terms.) (2) How is it done? What are the materials and methods, the techniques of data acquisition, the types of data analysis? (3) Why is it done? What is the purpose, objective, or goal; What is the overriding paradigm involved? How does the current study or topic relate to others? This simple W-H-Y method, first presented to me by one of my mentors, A. E. Radford, is useful to follow in any intellectual endeavor. It is a good lesson to teach one's students, and helps both in developing good writing skills and in critically evaluating a topic.

Finally, I would like to propose that each of us, instructors and students, pause occasionally to evaluate why it is that we do what we do. Over the years I have refined my ideas and offer these suggestions as possible goals: 1) to realize and explore the beauty, grandeur, and intricacy of nature; 2) to engage in the excitement of scientific discovery; 3) to experience and share the joy of learning. It is in this spirit that I sincerely hope the book may be of use to others.

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

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

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目 录

 		ix
孙谢		vi
双 闭]		741
	第一部分 系统学	
第1章	植物系统学: 概述	3
	但初系统字: 概述 ···································	
第2章	杀犹及 育 杀犹子 ···································	. 17
	第二部分 植物的进化与多样性	
第3章	绿色植物和陆地植物的进化与多样性······	• 55
第4章	维管植物的进化与多样性 · · · · · · · · · · · · · · · · · · ·	
第5章	木本植物和种子植物的进化与多样性	
第6章	有花植物的进化 ·····	
第7章	有花植物的多样性与分类:无油樟目、睡莲目、木兰藤目、木兰类、金鱼藻目和单子叶植	
第8章	有花植物的多样性和分类:真双子叶植物	275
	第三部分 系统学证据与描述性术语	
第9章	植物形态学 ·····	451
第 10 章	植物解剖学和植物生理学 ······	515
第 11 章	植物胚胎学⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯	545
第 12 章		561
第 13 章		
第 14 章		
77		
	第四部分 植物系统学信息资源	
第 15 章	植物的鉴定 ······	605
第 16 章		
第 17 章	植物的未集和吃来 ····································	
弗 18 草	标本馆和数据信息系统 ····································	637
	第五部分 物种概念和保护生物学	
第 19 章	植物系统学中的物种与保护 ·····	649
附录1	植物描述	
附录 2	植物学绘图 ······	
	植物系统学领域相关期刊	
	植物系统学中的统计学和形态测量学	
	-	
কংনা ''	(陈之端	
	(除之編	ナノ

CONTENTS

PREFACE	ix
ACKNOWLEDGMENTS	xi
unit I systematics	
CHAPTER 1 PLANT SYSTEMATICS: AN OVERVIEW	3
CHAPTER 2 PHYLOGENETIC SYSTEMATICS	17
unit II evolution and diversity of plants	
Chapter 3 evolution and diversity of green and land plants	55
Chapter 4 evolution and diversity of Vascular Plants	73
Chapter 5 evolution and diversity of woody and seed plants	129
CHAPTER 6 EVOLUTION OF FLOWERING PLANTS	163
Chapter 7 diversity and classification of flowering plants: amborellales, nymphaeales, austrobaileyales, magnoliids, ceratophyllales, and monocots	181
Chapter 8 diversity and classification of flowering plants: eudicots	275
unit III systematic evidence and descriptive terminology	
CHAPTER 9 PLANT MORPHOLOGY	451
Chapter 10 plant anatomy and physiology	515
Chapter 11 plant embryology	
Chapter 12 palynology	561
Chapter 13 plant reproductive biology	573
CHAPTER 14 DIANT MOLECULAR SYSTEMATICS	505

unit IV resources in plant systematics

Chapter 15 plant identification	
Chapter 16 plant nomenclature	611
Chapter 17 Plant Collecting and Documentation	627
Chapter 18 Herbaria and data information systems	637
unit V species concepts and conservation biology chapter 19 species and conservation in plant systematics	649
appendix 1 plant description	
appendix 2 botanical illustrations	675
appendix 3 scientific journals in plant systematics	679
APPENDIX 4 STATISTICS AND MORPHOMETRICS IN PLANT SYSTEMATICS	681
GLOSSARY OF TERMS	691
INDEV	725

I SYSTEMATICS



