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壳斗科植物花粉形态及生物地理

王萍莉　溥发鼎　著

Life

广东科技出版社

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NATIONAL NATURAL SCIENCE FOUNDATION OF CHINA

内容简介

本书首次全面介绍壳斗科各属的花粉形态及超微结构，内容覆盖壳斗科各属，除中国有分布的属种外，还包括分布于东南亚的轮叶三棱栎属，南半球的南美三棱栎属和南水青冈属，计9属160种，每个种有光镜照片，扫描电镜照片，关键类群做了透射电镜观察照相，或激光共聚焦分析，积累了4 000余张照片，并附有部分属种的植物标本照片，汇集为176个图版。

书中根据花粉形态的研究结果，综合相关学科，对科下系统、亚科划分、属间亲缘及系统演化等问题作了探讨，并有壳斗科各亚科和属的花粉形态检索表，是当代全面系统地记述壳斗科花粉形态及超微结构的一部专著。此外还论述了壳斗科的早期分化、生物多样性及生物地理。可供植物学、孢粉学、林学、植物地理学、地质学、历史植物地理学、古生物学工作者及大专院校相关专业师生参考。

Introduction

The present contribution of the pollen morphology and its exine ultrastructure features of *Fagaceae*.Altogether 160 species belonging to 9 genera are included in this book.It covers all genera in the *Fagaceae* that includes *Trigonobalanus* Forman from Southeast Asia,*Colombobalanus* Nixon et Crepet and *Nothofagus* Blume from Southern Hemisphere,besides Chinese native genera and species of *Fagaceae*.

The basic descriptive analyses are derived from observations by means of light microscope,scanning electron microscope,transmission electron microscope and laser scanning confocal imagine system(MRC-600).Four thousand or more photographes were taken by the authors who has spent over ten years,carrying out for this subject.It has compiled 176 plates in showing for the taxa.Some plates appended photographes of the specimens and a key of pollen morphology to the genera of *Fagaceae*,in order to will be attempted to identify them.

Based on the results of a study in characteristics of pollen morphology to divide infrafamily taxa,the intergeneric relationship,evolutionary trends and systematics are discussed.In addition to the early differentiation,biodiversity and biogeograph of *Fagaceae* are still under discussion.

The authors expect that this work is intended a reference of specialists who are engaging in palynology,systematics,geology, phytogeograph,environmental protection,ecology,palaeontology,forestry and other concened scientific and educational researches.

序

王萍莉研究员是现今国内少数几位现代孢粉学专家之一，十余年来专事壳斗科植物花粉形态研究，积累了大量新的资料，经她与合作者全面系统整理总结，集成本书。

中国是东亚乃至世界壳斗科植物的主要分布区之一，作者除全面研究中国壳斗科植物的属种外，还研究了东南亚地区和南半球的属种，对壳斗科各属160种进行了光镜、扫描和透射电镜观察分析，是迄今研究种数最多，方法较新的第一手资料，已处于国际先进地位。本书问世，是第一部全面系统记述壳斗科花粉形态和超微结构的专著，无疑将促进世界壳斗科特别是花粉形态的研究。

作者参阅了有关最新的资料，但又不拘泥于前人的观点，联系自己的研究和分析，结论有所创新，如：根据壳斗科的化石证据，首次提出壳斗科早期分化2个阶段的划分；揭示两半球壳斗科植物分别处于"华莱士线"东西两侧的分布规律；指出壳斗科植物在维护各类栎林生物多样性方面自然形成的突出作用。

壳斗科类群划分和系统演化问题，长期争议，无一定论。作者从花粉形态研究结果，联系比较形态学和古植物学，首先论证了南水青冈属归隶于壳斗科的观点，并进一步阐述了该属的原始性和独特性，从而建立南水青冈亚科；根据性状分析，探讨科下系统，提出4个亚科3个支系的演化趋势，根据充足，立论严谨，对过去壳斗科分类系统作了全面总结和新的调整，对壳斗科的系统进化，从孢粉学上提供了相当充分的证据，学术上有新的建树。

书中除汇编了176个图版外，还附有部分中国壳斗科植物标本照片，又精心完成壳斗科中各亚科、各属花粉形态检索表，将有助于辨认鉴别壳斗科植物，并为历史植物地理学、地层学、古生态学等提供重要参考。本书既对理论方法有所积累，又对有关生产有所启发和贡献，是一部双优之作。

吴征镒

2001年2月28日

前　言

壳斗科植物以其坚硬的壳斗状总苞包被坚果，形象地说明本科各属共有的特征，通常称之为壳斗科。

壳斗科植物广布于南北两半球，是组成热带、亚热带和温带森林的优势树种之一，在森林生态系统中起着突出的作用，在世界植物区系和植被组成中，占有显著的位置，第三纪以来，各地质年代地层中，壳斗科植物化石保存甚为丰富，是研究被子植物进化的重要类群之一，对于探讨第三纪孢粉组合，分析第三纪各时期植被类型及其所反映的气候特征具有重要的意义，各类壳斗林的木材和非木材森林产品，有较高潜在的经济价值，因而历来为植物学家、生态学家、林学家、地质、地理及古生物学家所关注。

自A.S.Oersted之后，一个多世纪过去了，经过几代植物学家的开拓、耕耘，不懈努力和潜心工作，壳斗科属种划分、科下系统、花粉形态、木材解剖、历史植物地理等方面有了卓著的成就，为我们对壳斗科的研究奠定了坚实的基础。

我们自1986年起，立项进行壳斗科花粉形态研究，先后获两项国家自然科学基金资助，“中国壳斗科花粉形态及超微结构”(1986～1988年)，及“三棱栎属、南水青冈属花粉形态及外壁超微结构”(1996～1998年)；中国科学院生物分类区系特别支持项目“壳斗科花粉超微结构及系统学”(1994～1996年)。研究内容涵盖壳斗科的各个属，以中国的属种为主，有水青冈属*Fagus* Linnaeus、栗属*Castanea* Miller、栲属*Castanopsis* (D.Don) Spach、石栎属*Lithocarpus* Blume、栎属*Quercus* Linnaeus[含青冈亚属subgen. *Cyclobalanopsis* (Oersted) Schneider]，以及分布于中国云南西南部和南部至泰国中部的三棱栎属 *Formanodendron* (Forman) Nixon et Crepet，还包括分布于印度尼西亚和马来西亚的轮叶三棱栎属*Trigonobalanus* Forman，以及分布于南半球的南美三棱栎属

Colombobalanus Nixon et Crepet和南水青冈属*Nothofagus* Blume，其中不少是中国的特有种，还有青藏高原、横断山区高山栎组的全部种类计12种；南水青冈属约35种，收集观察了27种，共计观察研究了壳斗科9属160种。

以壳斗科系统学中存在的问题及前人未曾观察的属种为研究重点，研究方法统一用Erdtman醋酸酐分解法，重视基本的光镜分析，并运用国际上观察花粉形态的先进手段，对壳斗科各属进行了扫描电镜观察，关键类群通过超薄切片在透射电镜下观察，或MRC-600型激光共聚焦系统分析。实验材料的收集处理、观察测试、整理总结，实验研究的全过程皆为笔者亲自所历，自1985年以来，陆续发表壳斗科花粉形态及超微结构的专题论文10篇，其中5篇作为阶段性研究成果，于1994年获中国科学院自然科学三等奖。

通过项目研究，积累了6 000余个测试数据，4 000余张光镜和各类电镜照片，观察分析数据翔实，研究的深度和广度超过了迄今国际上关于壳斗科花粉形态的研究工作，经过近几年对此项研究工作的系统整理总结，首次比较全面地介绍了壳斗科各属的花粉形态及超微结构。

根据地史资料，提出壳斗科早期分化的两个阶段，即晚白垩世—古新世的起始分化时期，始新世—渐新世各属分化形成时期。

综合有关壳斗科植物的外部形态、染色体数目、花粉形态、木材解剖、化石记录、地理分布等各分支学科的研究成果，论述壳斗科的生物地理及生物多样性，根据植物系统发育与地理分布相统一的原理，分析各属现存植物的分布式样，探讨类群的替代、散布，解释壳斗科现代分布格局的成因，类群分化与地质变迁的关系，揭示了壳斗科植物分布于北半球的7个属，与分布于南半球的2个属，正好处在“华莱士线”东西两侧，互不逾越这条生物地理分界线的规

律性认识。

生物多样性关系人类的生存与发展，书中阐述了各类栎林的现状，着重强调壳斗科植物在维护林内生物多样性的中心环节作用，控制着林中植物、动物、微生物资源的消长，决定着森林生态系统的稳定性，物华天宝，充分发挥壳斗科植物对保护生物多样性的重要作用，并赢得广泛共识，取得实效，是出版本书的目的之一。

运用比较形态学和古植物学方面的资料，探讨南水青冈属、三棱栎属(广义)、青冈属等的系统位置和科下系统，论述了南水青冈属仍隶于壳斗科下，以及建立南水青冈亚科的缘由；主张青冈属归并于栎属中，作为亚属处理；支持K.C.Nixon和W.L.Crepet建立三棱栎3个单型属；科下系统在A.S.Oersted壳斗科系统的基础上，作了新的调整。

壳斗科各类群花粉形态及超微结构的研究，取得了大量新的资料，结合系统发育分析和早期分化，讨论了壳斗科4个亚科分化为3条主干，形成3个支系的演化趋势。

本书共五章(见目录)，汇编了176个图版，图版中附有中国壳斗科部分属种的标本照片，丰富了本书的内容，此外还编写了各亚科、属的花粉形态检索表，上述努力旨在于提高本书的实用性和参考价值，提供可视性强的素材，便于鉴定壳斗科植物和地层中壳斗科的孢粉，加强和促进壳斗科的深入研究和学术交流。

我们首先感谢国家自然科学基金委员会，先后给予两项课题资助；中国科学院生物分类区系特别支持费的资助；国家自然科学基金研究成果专著出版基金委员会提供出版经费；中国科学院成都生物研究所提供编写费。

在书稿编排过程中，我们深深感谢中国科学院昆明植物研究所吴征镒院士热心推荐并为之写序，中国科学院植物研究所王文采院士赋予关怀推荐并祝贺鼓励，中国科学院南京地质古生物研究所宋之琛教授为本

书出版给予热情帮助和推荐。

王萍莉研究员从事花粉形态研究工作，得到中国科学院植物研究所张金谈教授的教诲和帮助，在壳斗科花粉形态研究的前期工作中，给予热情支持和悉心指导，谨此我们深表谢忱和对他的永远怀念。

我们在西南林学院标本馆工作期间，原西南林学院院长，著名的壳斗科植物分类学家徐永椿教授，指导壳斗科分类，提供花粉材料，我们怀着感激的心情，永远怀念他。

我们衷心感谢英国爱丁堡皇家植物园、伦敦邱皇家植物园标本馆的同事们，对我们工作和生活上的热情关照，提供有关文献资料、花粉材料、光学显微镜和照相器材，安排扫描电镜观察，良好的工作条件，使我们能够研究南半球和东南亚地区的壳斗科植物，拓宽研究壳斗科的视野，对壳斗科的属种有比较全面的认识。

我们深切感谢中国科学院植物研究所孔昭辰研究员百忙中提供壳斗科植物的化石记录，本所郑中华研究员参与壳斗科一些属种外壁超微结构的出色工作；本所《应用与环境生物学报》编辑部为本书制作部分插图。

面对壳斗科这一大题目，错误、片面性实为难免，其中的学术问题看法也不尽一致，敬请读者正之。

作者于成都

2003年1月25日

Preface

The nuts is invested by the hard cupulate involucre.This character used to unite the all species of *Fagaceae*.

The oak family (*Fagaceae*) widely distributed in both of the Northern and Southern Hemispheres except the most areas of Africa. It displays with frequent dominance element in the tropical,subtropical and temperate forests.*Fagaceae* lies in distinquished position within the flora and vegetation of the world,and it play a dominant role in ecologyical system of forest.

Various fagaceous mountain forests are over large areas thereby producing a colossal biomass,possibly a good second after the conifers.The timber source and non timber forest products have higher potential economic value therefor they have frequently captured the interest of botanists,ecologists,foresters,geographers,and paleontologists.

It has been past for more than a century after A.S.Oersted.Former botanists pioneered work on *Fagaceae* and with splendid achievements in external morphology,characters of plant growth habits, pollen morphology,wood anatomy,some chromosomal number, embryology,phytogeography,generic and specific divisions,systematics and evolution,etc.All of these have laid foundation for our studying on this field.

The authors have studied on pollen morphology of *Fagaceae* since 1986.Two subjects that grants were given by National Natural Science Foundation of China,i.e."pollen morphology and exine ultrastructure of *Fagaceae* in China"(1986~1988),and "Pollen morphology and exine ultrastructure of Trigonobalanus Forman(s. l.)and *Nothofagus* Blume"(1996~1998).A subject,"pollen exine ultrastructure and systematics of *Fagaceae*" (1994~1996)was supported by Toxonomic and Floristic Special Grants of the Chinese Academy of Sciences.

The present work covers all genera of Fagaceae i.e.*Fagus* Linnaeus,*Castanea* Miller,*Castanopsis* (D.Don)Spach,*Lithocarpus* Blume,*Quercus* Linnaeus(s.l.),and *Formanodendron* (Forman) Nixon et Crepet,but chief among of the materials were from China,where

some species endemic to China,some species from Qinghai-Xizang plateau and the whole section *Brachylepides*,12 species from Hengduan Mountains of southwest China were comprised. Otherewise still include two monotypic genera,i.e.*Trigonobalanus* Forman(s.str.)from Indonesia and Malaysia,*Colombobalanus* Nixon et Crepet from Colombia of South America.A genus Nothofagus Blume of about 35 species which 27 species were observed.It was from Southern Hemisphere in South America,east Australia,New Zealand,Tasmania,New Caledonia and Nwe Guinea. Altogether 160 species,belonging to 9 genera are included in this book.

Pollen grains of some genera in *Fagaceae* were collected by the authors during field work in southwest China,recent 20 years,and a part removed from herbarium sheets deposited at the Herbarium of Chengdu Institute of Biology,the Chinese Academy of Sciences (CDBI)and Herbarium of South West Forestry College,China (SWCF).The pollen grains of *Trigonobalanus* Forman(s.l.) *Colombobalanus* Nixon et Crepet and *Nothofagus* Blume were provided by Herbarium of Royal Botanic Garden Edinburgh(E) and Herbarium of Royal Botanic Gardens Kew(K).

Pollen grains for light microscope(LM)observation were prepared by Erdtman's acetolysis method.Acetolysed pollen grains were mounted in glycerin jelly and their sizes were calculated from 15~20 per sample.For scanning electron microscope(SEM),the pollen grains were vacuum coated with gold palladium and observed directly with SEM JSM-35 S 11.Pollen section for trasmission electron microscope(TEM) were prepared by normal ultrastructure thin sectioning technique(Zhang Zhong-Hua,1988)and observed with TEM,JEM-100CX,or using laser scanning confocal imagine system MRC-600 to observe.

Professor Wang Pingli who has spent over ten years carrying out for this subjuct from experiment,measure,observation,analysis, taking photomicrograph to description,almost by herselves,as well as,cooperated with technologists on SEM or TEM.It has accumu-

lated six thousand or more experimental data and over four thousand photomicrographes.Pollen morphology and ultrastructure of *Fagaceae* concened,the authors have published ten papers which five papers won third-class Natural Science prize of the Chinese Academy of Sciences.This book attempts to provide more useful information based mainly on the authors firsthand materials,and an overall,concentration nine genera of pollen morphology and ultrastructure of *Fagaceae* is presanted for the first time,Some important problems in the systematics of *Fagaceae* are discussed,and the authors are proposed in this book.

Based on the fossils data,the early differentiation of *Fagaceae* may be divided into two stages:(1)Initial stage was from Late Cretaceous to Paleocene.(2)Flourished stage,or all genera of *Fagaceae* formation stage was from Eocene to Oligocene.

The authors who remarked the biogeograhy and biodivrsity of *Fagaceae*.On the basis of unity of the phylogeny and the process of dispersal in plants,the distribution patterns of living genera including their replacement,migration,dispersal,and cause of formation of distributional patterns are analysed. The differentiation of fagaceous grups has been related to the geological change.The distributional area of the seven genera in Northern Hemisphere and two genera in Southern Hemisphere lie in the both side of west and east of "wallace's line".They have not gone beyond the limits of this famous biogeographic line each other.

The authors expounded their views on the status of the fagaceous forest,which is an important link for protecting biodiversity in the forest.It regulates retreat and development of the forest resources in plants,animals and microbes and controls the stability of the forest ecosystem.

Cyclobalanopsis Oersted treated as a subgenus under the genus *Quercus* Linnaeus.*Trigonobalanus* Forman(s.l.),well supports the viewpoint of K.C. Nixon and W.L.Crepet to treat as three monotypic genera,i.e.*Formanodendron*(Forman) Nixon et Crepet, *Trigonobalanus* Forman(s.str.),and *Colombobalanus* Nixon et

Crepet,they are confirmed by the synthetic data of poilen morphology and other characters.The genus *Nothofagus* Blume shares various ecological features,many morphological characters and growth habit quite allied with the most of genera of *Fagaceae*.As remarked above,it is closely allied to *Fagaceae*,so the genus *Nothofagus* Blume is an undoubted member of the *Fagaceae*.The authors are recolled that have supported the genus *Nothofagus* Blume to exclude from *Fagaceae* in 1999,and now support it retention in *Fagaceae*.Nevertheless,it quite distinct in pollen many morphological characters really differs from the other genera of *Fagaceae*.Several evidences are suggested to give a higher taxonomic rank that it is treated as a subfamily to describe and discuss.The classification is based on phylogenetic analyses and differs somewhat from previous subfamilial and generic classifications of this family.The position of all the genera within the *Fagaceae* are further adjusted.It maybe proposed to divide four subfamilies and formation a frame of three evolutionary boughes system.

This book is divided into five chapters. It has compiled 176 plates in showing for the taxa.Some plates appended phtographes of the specimens.With a key of pollen morphology to the genera of *Fagaceae* was added.

In an unusual degree,this work is the fruition of a cooperative effort on the part of many persons and the staff members of several libraries and herbarias.

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Only limited studies have been made of the pollen morphology, biodiversity and biogeograph of Fagaceae.One reason for this lies in our very incomplete knowledge of the systematic botany and so on in this great subject of *Fagaceae*.

Authors
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祝《壳斗科植物花粉形态及生物地理》出版

了解被子植物及其所属各科的系统发育及如何分类，在研究历史早期，主要依靠形态学的特征进行分类，以后其他植物学分支学科相继出现，这些方面的综合研究大大促进了上述有关研究。在这些分支学科中，孢粉学做出了重要贡献。从20世纪中期起，孢粉学在被子植物系统发育方面的研究突飞猛进，取得了大量研究成果，解决了不少在系统发育、亲缘关系等方面的疑难问题。像近年来发表的被子植物分类系统，主要利用花粉萌发孔的数目便可区分出原始群(具单孔或单沟花粉)和进化群(具三孔或三沟花粉及其衍生类型)就是一个例证。我国的孢粉学研究主要在解放后才开始展开工作，在改革开放后突然出现了一个研究高潮。在近20余年中，发表了大量著作，涌现出不少孢粉学家，本书的作者之一，中科院成都生物研究所王萍莉教授就是其中的一位。王教授在近二十年中与合作者先后研究了白花丹科、壳斗科、伞形花科，以及横断山区一带植物的花粉，发表了大量高水平的论文和专著。最近，她与合作者溥发鼎教授一起对组成热带至温带森林的壳斗科植物的花粉形态、生物多样性、生物地理及科下各属的分类位置与系统演化，继续进行了全面、深入的研究，根据南水青冈属(Nothofagus)的花粉形态及超微结构、胚胎学性状、染色体数目与壳斗科其他各属的比较，进一步认为此科各属的亲缘关系，基于南水青冈属的胚珠为单层珠被，花粉外壁特征，以及晚白垩世桑托尼期的化石记录，认为南水青冈属是此科分化较早的原始群。本书作者根据这些新的研究成果，对壳斗科各属做出了新的分类处理。这一新的分类系统更好地表现出壳斗科各群的亲缘关系，对壳斗科系统发育研究做出了新贡献。看到她们的新贡献，我感到很高兴，谨在此对《壳斗科植物花粉形态及生物地理》一书的胜利完成和出版，表示我衷心的祝贺！

王文采

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