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中国主要经济植物基因组

染色体图谱

第三册

中国园林花卉植物染色体图谱

陈瑞阳 宋文芹 李秀兰 著
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CHROMOSOME ATLAS

OF MAJOR ECONOMIC PLANTS GENOME IN CHINA

Tomus III

Chromosome Atlas of Garden Flowering Plants in China

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内 容 简 介

本书为《中国主要经济植物基因组染色体图谱》的第三册,收录了作者对我国64科205属356种园林花卉植物染色体研究的资料。其中包括染色体的数目、倍性、核型分析的基本数据。这些染色体的基础科学数据不仅对花卉的杂交育种、细胞分类、起源进化研究具有重要理论意义和应用价值,而且也是园林花卉植物基因组研究的重要依据。

本书可供园艺、林业、生物等专业的高等院校教师、研究生和相关科研院所的研究人员及生产技术部门参考。

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郝 水 序

人类对染色体 (chromosome) 的认识已经有一百多年的历史。在 18 世纪中叶已经出现关于染色体的描述。据文献记载,最早描述染色体的是 Nageli(1842),他绘制的是紫露草 (*Tradescandia*) 花粉中的染色体,但当时他并未使用染色体这个名词。“染色体”名词是 W. Waldeyer 于 1888 年在一篇发表在德文期刊上的论文中提出的。它是指细胞中一种碱性染料浓染的小体,德文称之为 Chromosomen(复数)。1926 年,美国学者 Morgan 通过对果蝇的遗传研究,得出连锁交换定律,并确定主管生物性状遗传的基因直线排列于染色体中。人们自然把探求遗传物质的分子基础集中在染色体的研究上。后来生物化学的研究表明,染色体中存在核酸和蛋白质两类分子。1944 年, Avery 等从肺炎双球菌的转化实验中证明,转化因子是脱氧核糖核酸 (DNA),而不是蛋白质。1953 年, Watson 和 Crick 提出了 DNA 双螺旋模型,以及随后根据其他发现,终于确定了 DNA 作为基因分子实体的认识。

既然染色体中除 DNA 外还存在大量蛋白质,那么,染色体中的蛋白质起什么作用呢?研究表明,染色体中蛋白质有两类,一是组蛋白 (histone),二是非组蛋白质 (nonhistone protein, NHP)。前者有 H2A、H2B、H3、H4 和 H1 五种蛋白质。其中,前四种蛋白质各二分子聚合成八聚体,称为核小体核心。核小体核心与 DNA 结合,成为串珠样染色质链 (A. L. Olins and D. E. Olins 1973, 1974)。NHP 种类繁多(至少有 30 余种),且富变化。它们构成染色体的骨架结构 (U. K. Laemmli 1978)。近 20 余年的研究表明,这两类蛋白质对 DNA 的基因转录、复制、重组、集缩与解集缩等功能,以及染色体的构型均有重要调控作用,此外,近 20 余年的研究还表明,中期染色体周围还有一个由核糖核蛋白 (RNP) 构成的表层,但对这个 RNP 表层染色体 DNA 的功能意义尚缺乏了解。

从人类对染色体百余年的研究结果可以看出,每条染色体中不仅有作为遗传密码的 DNA 大分子,而且有参与调控 DNA 实现遗传功能(基因转录表达、复制、重组和集缩传代)的种类繁多的蛋白质。

染色体通常是在细胞周期的分裂中期形成的高度集缩的结构,它是由直径为十多纳米核小体链经过 4~5 级逐次集缩形成的。其直径约 1000 纳米,每种生物体的体细胞都有一定数目的染色体,并且染色体的大小和形态(长度、直径、着丝粒位置及其他特征)都各具特点。它们是不同的物种基因组的最简单明了的形象表现。

南开大学生物系陈瑞阳教授及其研究集体和合作者在植物染色体制片技术方面卓有成就,并多次举办全国性染色体技术学习班,培训了大量专业人才,促进了我国植物染色体组型的形态学研究蓬勃发展。20 多年来,陈瑞阳教授及其同事积累了大量有关我国经济植物染色体组型的文字和图像资料。他们和其他单位的同行编著的《中国主要经济植物基因组染色体图谱》共分四册,包括果树、农作物、园林花卉和竹类植物。仅果树

方面就包括了29科52属261种。非常可贵的是果树和农作物中还包括了它们的野生近缘植物的染色体图谱。这一套图谱的学术和应用价值是十分明显的。它为我国重要经济植物的基因组学,尤其是功能基因组学的研究提供了系统的直观基础资料。它对研究我国重要经济植物遗传、起源和进化,特别是品种改良的育种实践具有重要意义。这套图谱是迄今国内未曾有过的,与国际上的同类著作相比是先进的。

在此图谱出版之际我谨向作者们表示衷心祝贺。

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郝水

2002年2月5日

Preface by Hao Shui

Chromosomes have been recognized for more than a century. As early as the middle of the 18th century, the description of chromosomes was reported. According to historical records, the chromosome was first described by Nageli (1842), based on his observations of *Trandescantia* in the process of pollen development. However, he did not use the term "chromosome" at that time. "Chromosome" was coined by W. Waldeyer (1888) and first appeared in his published paper in a German journal; "chromosome" was used to describe a tiny rodlike structure stained by alkaline dye. In Germany, it was known as Chromosomen (pl.). In 1926, Thomas Hunt Morgan, an American scientist, proved the linkage and cross-over law based on the data from his experiments with fruit flies. He confirmed that the genes which carried the blueprint for life were situated within chromosomes. Naturally, research work on the molecular basis of hereditary material, thereafter, became focused on the study of chromosomes. Later, biochemical discoveries indicated that there were two kinds of molecules in chromosomes: nucleic acid and protein. In 1944, O. T. Avery and his coworkers demonstrated that the transforming factor was DNA rather than proteins derived from *Streptococcus pneumoniae* transforming experiments. In 1953, Watson and Crick proposed the double-helix structure of DNA. Along with other notable discoveries, DNA was finally regarded as bearing the hereditary molecules of the gene.

Given that there are a great number of proteins in addition to DNA in the chromosome, what are the functions of these proteins? Studies have demonstrated that there are two kinds of proteins in chromosomes: one is histone, the other is nonhistone (NHP). The former includes five kinds of proteins: H2A, H2B, H3, H4 and H1; among these proteins, two molecules each of the former four kinds of proteins revolve around a core histone octamer, known as the nucleosomal core. The nucleosomal core interacts with DNA to form solenoid chromatin fiber (A. L. Olins and D. E. Olins 1973, 1974). The types of NHP are numerous (more than 30), and exist in large numbers of variegating strains. They constitute the skeletal structure of the chromosome. Studies over the past twenty years have demonstrated that both histone and NHP play an important role in gene transcription, replication, recombination, condensation, decondensation, and chromosomal configuration. Furthermore, these studies also discovered the existence of a surface layer constituted by ribonucleoprotein (RNP) around the chromosome at metaphase. However, we are far from fully understanding the function of this RNP surface layer tightly bound to chromatin.

From the findings of more than a century of study on chromosomes, the individual chromosome contains not only DNA macromolecules as hereditary codes but also various proteins involved in adjustment of DNA pre-hereditary functions (gene transcription, expression, replication, recombination, condensation, and generation).

Basically, a chromosome is a highly condensed structure at metaphase of the cell cycle. It is constructed by 10 nm filament of nucleosomes following 4 – 5 steps of condensation and has a diameter of 1000 nm. The somatic cells of an individual have a given number of chromosomes, and their size and shape (length, diameter, centromere position, and other characteristics) have individual specificity. There are simple and clear image expressions of genome in different species.

Professor Chen Ruiyang and his research group in the Department of Biology, Nankai University, have made outstanding contributions in the field of plant karyotype preparation techniques. They have conducted several national training courses for these preparation techniques for many professionals and, thereby, have promoted a vigorous stimulus for development of plant chromosome research in our country. Over the past twenty years, Professor Chen and his colleagues have collected a great deal of literature and pictorial data on karyotypes of economic plants in our country. *Chromosome Atlas of Major Economic Plants Genome in China*, is divided into four volumes, covering fruit trees, crops, horticulture plants, and bamboo species. In the field of fruit trees alone, the atlas includes information on 261 species in 52 genera from 29 families. It is a praiseworthy endeavor that wild kindred plants are included in the atlas volumes of fruit trees and crops; the academic and applied values are self-evident. There is a significant supply of systemic objective basic data for important economic plant karyology, especially functional karyology. This is essential in research concerned with economic plant heredity, origin, evolution, and, especially, breeding practices for improving plants. This atlas, provides advanced information in comparison with similar international publications.

The authors are offered my hearty congratulations on the occasion of the publication of this atlas.

Academician Hao Shui

Chinese Academy of Sciences

Professor of Northeast Normal University

Feb. 5, 2002

杨弘远和周嫦序

我们和陈瑞阳先生相识，最早是在20世纪60年代初。当时我们大家都是初出茅庐的青年，初生牛犊不怕虎，怀着在中国科学事业中做出一番贡献的抱负。可惜好景不长，“文革”十年浩劫打破了我们的理想，中断了我们刚刚起步的研究工作。粉碎“四人帮”和改革开放迎来了我国科学事业的春天。当时陈瑞阳和我们都是霜染两鬓的中年人了，然而一股不可遏止的激情驱使我们投入新的研究事业，要将失去的年华抢回来。1979年，中国植物学会委托南开大学生物系举办首次全国染色体技术学习班，我（杨弘远）有幸参加并在会后出版的一本册子中与陈瑞阳合写了一篇文章。其实，我在这一方面只是“纸上谈兵”，而他则是“真刀真枪”地干，而且一干就是二十几年。以后，虽然我们和他的研究方向各不相同，但始终互通信息、互相支持。我们敬佩他在学术工作中脚踏实地、始终如一的奋斗精神，也从他的成就中分享一份快乐。

众所周知，染色体是遗传信息的载体，基因只有组织在染色体上才能在遗传上发挥作用。当今，基因组研究是生命科学中最热门的领域。接下来，分子水平的研究还必须与细胞水平的研究结合起来，从细胞到分子再回到细胞，这是生命科学发展的趋势。由陈瑞阳教授等著的这部植物染色体图谱，包括90科、267属、945种植物的1200幅染色体图版，是集他本人及其研究集体几十年心血完成的一部巨著。它填补了世界植物染色体图谱的空白，体现了我国学者在这一研究领域的重大贡献，可以说是一部传世之作。

科学的发展离不开实验技术的更新。以往的染色体压片技术，很难对付染色体数目众多、体形较小的材料。陈瑞阳教授创造性地提出去壁低渗法，大大提高了植物染色体制备的质量，成为他们这部染色体图谱的主要方法学基础，但他不满足于核型分析，又提出了植物染色体G-带技术等一系列分带方法，使植物染色体研究进入了更微观的阶段，这在本书中也均有所展现。近年，陈瑞阳教授又在朝新的高度进军，实现了染色体微切割、分离与克隆等更精密的实验操作，预示了植物染色体工程新阶段的来临。

我们衷心祝贺本书的问世。

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杨弘远

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周 嫦

2001年12月31日

Preface by Yang Hongyuan and Zhou Chang

It was in the early 1960s that we first met Mr. Chen Ruiyang. Although young and inexperienced at that time, we were both fearless and dedicated in our pursuit of scientific research in China. But this didn't last long. Our hopes were destroyed during the ten-year "Cultural Revolution" and our research was suspended in the initial stages. Subsequently, the overthrow of the "Gang of Four" and introduction of reform and open-door policy in China restored scientific research to its full bloom. Although each of us, including Ruiyang, had reached middle age by that time, we were still encouraged and, with irresistible enthusiasm, immersed ourselves in our new research; we vowed to utilize our time wisely and to overcome the deficit in valuable research time lost over the years.

In 1979, the China Plant Association assigned the Department of Biology, Nankai University to hold the first national course on chromosome technology. I (Yang Hongyuan) was honored to be involved in presenting the class and co-wrote with Prof. Chen a paper subsequently included in the colloquia for participants. Following our collaboration, we continued to maintain contact and encouraged each other over the years despite of the fact that we pursued research in different fields. Admittedly, I was an armchair strategist in this field while my colleague persisted in real earnest in his efforts for over twenty years. Chen is highly regarded for his practical and consistent attitude toward academic work. We are delighted with his achievements.

It is recognized that the chromosome is the bearer of genetic information. Only when the gene is sited on the chromosome can it function in heredity. Currently, life sciences are focused on genomic research, but research at the molecular and cellular levels also needs to be included. The research focus shifts from cell to molecule and then back to cell, which is the trend in scientific development. This chromosome atlas of plants edited by Professor Chen includes 1200 chromosome plates of 945 species in 267 genera, representing 90 families, a great accomplishment by Chen and his research colleagues over two decades. It eliminates a knowledge gap with the chromosome atlas of plants in the world and presents the great contribution made by these researchers within this field in China. This outstanding work will certainly be passed on from generation to generation.

Without updating experimental technology, science would never continue in its development. It was difficult to deal with plant materials that have numerous chromosomes of small size using the previous karyotype preparation technology. Professor Chen creatively proposed "walls degradation hypotonic" methods, which greatly improved the quality of preparation of plant karyotypes. This methodology forms the basis for the methodology used within this chromosome atlas. Not satisfied with karyotype analysis, Chen also proposed a series of banding methods such

as plant chromosome G-banding technology enabling plant chromosome research to enter an even more microcosmic stage as demonstrated in this atlas. In recent years, Professor Chen continued his research and created more precise experimental procedures such as chromosome microdissection, separation and cloning, introducing a new era in the future of plant chromosome engineering.

We express our hearty congratulations in recognition of Prof. Chen's years of laborious research with his colleagues and in the publication of this atlas.

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Dec. 31, 2001

洪德元序

染色体是基因的载体，它控制遗传和变异，并支配生殖和发育，而染色体自身的数目、形态结构和行为也受基因的调控。对染色体的研究，从结构与功能、行为和进化而言，既可以指向过去，也可以分析它的现在和预测它的将来，由此，发展了细胞遗传学、细胞分类学和物种生物学及近年蓬勃发展起来的分子细胞遗传学。人类基因组和作物基因组的全序列测定，更成为21世纪生命科学的里程碑。上述学科从不同层次、不同角度开展研究，都是以染色体组的组成（一个或多个基因组）和结构为基本单位，或者甚至以单个染色体的识别为基础的。陈瑞阳教授等著的《中国主要经济植物基因组染色体图谱》正是提供了这方面的重要基础资料，它对上述各学科的研究都有重要参考价值，它是生命科学中的基本建设之一。

我国的植物染色体研究，起步较晚，20世纪80年代以前几乎是空白，改革开放后，在南开大学生物系、北京大学生物系、中国科学院植物研究所和中国农业科学院等单位的参与和组织下，相继在南开大学和全国各地举办了各种学习班和国内外的学术研讨会，促进了我国植物染色体研究的蓬勃发展，无论在研究范围和深度上，还是在研究技术水平上我国都已接近或达到世界先进水平。其中，以陈瑞阳教授为首的南开大学植物染色体实验室，20年坚持不懈、辛勤工作，投入极大的精力和热情，以及对我国科学事业的责任心，不辞辛苦，跋涉全国各地，采集和征集材料，并以精湛的染色体技术做出每一物种的染色体制片，拍摄出精美的照片，测出详细的核型参数，汇编成四册《中国主要经济植物基因组染色体图谱》。它的出版是值得赞许和庆贺的，它不仅在国内是首部原创巨著，在国际上也填补了该领域的空白，必将引起广泛关注。

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洪德元

2001年12月15日

Preface by Hong Deyuan

The chromosome is the bearer of genes that control not only heredity and variation, but also reproduction and growth. The number, structure, and behavior of chromosomes are also adjusted and controlled by genes. As far as the structure and function, and behavior and evolution are concerned, chromosome research not only focuses on the past, but also analyzes the present and forecasts the future. Consequently, cytogenetics, cytotaxonomy, biosystematics, and molecular cytogenetics have received much attention and have been vigorously developed over the past several years. Moreover, the completion of the draft sequences for human and plants genome has marked a milestone for life sciences in the 21st century. In researches at different levels and aspects in the above-mentioned areas, the composition (one genome or more) and the structure of the genome are considered as a basic unit or based on identification of a single chromosome. *The Chromosome Atlas of Major Economic Plants Genome in China* compiled by Professor Chen Ruiyang provides an important basis as a research reference for the above-mentioned disciplines; it highlights one of the basic developments in the life sciences.

In China, plant chromosome research began not long ago and no significant research was carried out before the 1980s. Following the introduction of reforms and the open-door policy in China, various study classes in addition to both domestic and international seminars were held in Nankai University and various regions throughout the country. These educational and informative sessions were organized and participated in by the Department of Biology, Nankai University; the Department of Biology, Peking University; the Institute of Botany, Chinese Academy of Sciences and the Academy of Agricultural Sciences of China. These ventures promoted the rapid development of plant chromosome research. Therefore, regarding the extent and depth of research or technical expertise in this field, China has approached or reached the advanced world standard. Among leading researchers, Professor Chen Ruiyang, head of the Plant Chromosome Laboratory at Nankai University, together with his colleagues, researched relentlessly, vigorously, and enthusiastically in China for the past 20 years. They conscientiously and painstakingly gathered plant specimens from the various regions of China. Their work has been documented with photos of chromosomes from each species with superior chromosome technology and exquisite photographic pictures. Detailed karyotype parameters were determined and four volumes of *Chromosome Atlas of Major Economic Plants Genome in China* were then compiled. This publication deserves the profound appreciation and congratulations from its readers for the work it represents and the value of its contents. This atlas is not only an original great work

domestically, but also a resource that fills a gap in plant chromosome research internationally. It will undoubtedly attract widespread attention.

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自1888年Waldeyer命名染色体(chromosome)以来,有关染色体与染色体组(基因组)结构与功能的研究,一直是生命科学最活跃的研究领域之一。2000年6月26日,人类基因组第一个测序图公布后,更让人们兴奋,人类从何而来又向何处去的奥秘即将被揭开,基因在染色体上排列的空间结构也将展现在世人面前,人类将进入一个多学科交叉的生命科学时代。然而,任何一门学科的兴起,都有它由长期的量变积累到质变的飞跃过程,染色体研究更是如此。从1882~1956年的70多年间,经过无数科学家的不懈努力才搞清楚人类染色体数目为 $2n=46$,而不是 $2n=48$ 。随着染色体技术的不断发明和完善,特别是20世纪50年代初期低渗法的发现,包括人类在内的高等哺乳动物染色体研究取得了长足进展;1960~1970年10年间连续四次召开国际会议,确定了一系列人类染色体分析的国际统一标准。T.C.Hsu花了10年时间主编了世界第一部哺乳动物染色体图谱(*Atlas of Mammalian Chromosomes*),使涉及以染色体为基础的学科,如细胞生物学(Cell Biology)、细胞遗传学(Cytogenetics)、细胞分类学(Cytotaxonomy)、细胞地理学(Cytogeography)和物种生物学(Biosystematics)等领域得到了极大的发展,也为后来的分子生物学和基因的染色体定位奠定了良好的基础。然而,植物染色体研究虽然在20世纪三四十年代有过先驱作用,但自1950年以后,与动物染色体研究相比发展较为缓慢,至今除了几本专门记载植物染色体数目的书刊[如(1)C. D. Darlington and A. P. Wylei(1955), *Chromosome Atlas of Flowering Plants*; (2)C. D. Darlington and E. K. Janak Ammal(1945), *Chromosome Atlas of Cultivated Plants*; (3)Peter Goldblatt, *Index to Plant Chromosome numbers*; (4)V. L. Komarov (1969), *Chromosome numbers of flowering plants*]外,还没有一本可与哺乳动物染色体图谱相近的植物染色体图谱出版。本人及所领导的实验室,自建立植物染色体的去壁低渗法(陈瑞阳等1979,1982)后,就立志编著《中国主要经济植物基因组染色体图谱》。

在20世纪五六十年代,由于染色体各种新技术的应用,在国际上,染色体研究达到了鼎盛时期。然而,我国植物染色体研究由于种种原因起步很晚,1976年以前除我国台湾省外,基本处于空白状况,由中国人(除台湾省和外籍华人外)自己首次鉴定的植物染色体数目和核型分析资料基本没有。这与我国的地位和占有的丰富植物资源种类是极不相称的。中国植物学会委托南开大学生物系染色体实验室于1979年和1981年两次举办全国(300多个单位参加)植物染色体技术学习班后,我国的植物染色体研究才进入蓬勃发展的阶段。据不完全统计,1979~1989年共发表有关植物染色体论文约600篇,涉及的植物种类近3000种(徐炳声1986,1988,1989),1984年8月在辽宁兴城召开了第一届全国植物染色体学术讨论会,1986年在河北省昌黎举办了第三次植物染色体技术学习班,1987年在北京香山召开了第一届中日植物染色体学术讨论会,1992年在南开大

学召开了第二届中日植物染色体学术讨论会，并出版了植物染色体学术讨论会论文集。上述学术活动，对我国植物染色体研究的发展起到了极大的促进作用，同时也展现了我国植物染色体研究在染色体标本制备的去壁低渗法、Giemsa C-带、N-带、G-带、银染和核型分析等方面都有所改进和创新，在诸多方面达到了国际先进水平。这不仅显示我们只用了10多年的时间填补了我国植物染色体研究100多年来的空白，而且也为我国植物染色体研究的深入发展奠定了坚实的基础。

本套染色体图谱，就是在上述背景条件下，以本人为首的南开大学染色体实验室的全体同事，在国内著名的植物染色体专家李懋学先生、林盛华研究员、梁国鲁教授积极参与和鼎力相助下，经过20多年的不懈努力完成的。在研究材料的选择上，我们从中国30 000种高等植物中，选择了具有重要经济价值和理论意义的栽培植物及其野生近缘种，特别注重搜集原产我国的栽培植物及其野生祖先种。在染色体研究技术方面除少数材料使用压片法外，本图谱绝大部分材料均应用去壁低渗法制备染色体标本，染色体分散、平整、易测量，核型分析采用统一的分析标准，并由计算机编程软件计算，减少了人为误差。同时，本图谱结合具体材料，应用了各种分带技术，如C-带、N-带、G-带，Ag染和rDNA原位杂交，荧光原位杂交(FISH)等最先进的染色体技术，使本图谱的结果达到了国际先进水平。

《中国主要经济植物基因组染色体图谱》一套共四册：

第一册 《中国果树及其野生近缘植物染色体图谱》。

第二册 《中国农作物及其野生近缘植物染色体图谱》。

第三册 《中国园林花卉植物染色体图谱》。

第四册 《中国竹类植物染色体图谱》。

本图谱的出版不仅对研究栽培作物的起源、进化、遗传育种具有重要的理论意义，而且对栽培作物基因组计划的实施、遗传图谱的绘制、基因的染色体定位等也具有重要的应用价值。

本人及所领导的染色体实验室，自1985年起曾先后13次获得国家自然科学基金资助，为本书的编著奠定了基础。本次又获得国家自然科学基金研究成果专著出版基金的资助，才使这项基础性很强的科学专著得以问世，实在是一件值得庆贺的事！在整个图谱的筹划和出版过程中，得到我们的师长和老友周嫦教授、杨弘远院士（武汉大学），郝水院士、何孟元教授（东北师范大学），郑国锴院士（兰州大学），洪德元院士（中国科学院植物研究所），翟中和院士、朱澍教授（北京大学），吴小航教授、张玉玲教授、周之杭教授、张自立教授（南开大学）的关怀和鼓励，同时也得到日本广岛大学原校长，本人的博士生导师田中隆庄教授的指导，在此表示诚挚的谢意！

陈瑞阳

于南开大学

2001年11月30日