



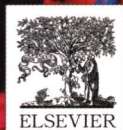
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# The Evolution of the Genome

# 基因组的进化

T. Ryan Gregory



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# The Evolution of the Genome 基因组的进化

F. M. Smith



WILEY

**THE EVOLUTION OF THE GENOME**

# **基因组的进化**

Edited by  
T. Ryan Gregory

**科学出版社**

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## 导 读

随着基因组研究技术的迅猛发展,我们已经积累了海量的基因组数据,而且未来还会产生更为庞大的基因组数据。如何解读这些海量数据,理解生命的本质,成了后基因组学时代的一个巨大挑战。基于比较方法的进化基因组学研究无疑将成为解读这些海量数据的一个十分有效的手段。但是,有关基因组进化研究的历史、现状和未来一直都缺乏一个完整而系统的描述,有关其研究内容也十分模糊。《基因组的进化》这本书通过邀请一批相关领域的著名学者,包括美国科学院院士 Margaret Kidwell 和亚利桑那大学分子进化学家 Sudhir Kumar 等著名科学家,首次全貌式地介绍了基因组进化研究的各个方向和领域。内容涉及基因组组成、结构及其进化,基因组进化与一些重要生物学问题的关系,以及通过比较基因组学研究理解基因组结构和功能进化的型式和机制等。

本书共分 5 个部分 11 章内容。第一部分从 C 值悖论讨论了动植物基因组大小进化的问题;第二部分介绍两类寄生的遗传因子:转座子和 B 染色体(相对于正常染色体组的超数染色体);第三、四部分着重讨论基因和基因组重复这一重大问题;第五部分主要体现了本书的编者 Ryan Gregory 博士对整合基因组水平的进化与宏观水平上的生物进化理论的思考。

具体而言,第一章从作为遗传物质的 DNA 发现开始,首先介绍了著名的 C 值悖论,即 DNA 含量并不总与生物复杂性呈正相关,然后介绍了现有动物基因组大小的数据库,基因组大小变异的型式和机制,特别是对机制给予了详尽的解释,随后讨论了基因组大小与细胞、生物体大小及代谢和发育等的关系,最后描述了测量动物基因组大小的方法和有关动物基因组大小研究的展望。

第二章在介绍植物基因组大小研究的历史和现状的基础上,基本沿用了第一章的结构,讨论了植物基因组的大小问题。所不同的是,植物中存在大量的多倍体,从而导致了种内和种间基因组大小的广泛变异。

第三章由世界著名的转座子研究专家 Margaret Kidwell 教授写就,权威性地介绍了转座子研究的历史、转座子的分类、结构特征和研究方法,转座子在遗传学研究中的应用,转座子自身的进化过程和对基因组进化的影响。

第四章介绍了在流行的基因组学知识中很少涉及的一个重要寄生因子,B 染色体。本章介绍了 B 染色体的物种分布、大小、结构、组成和奇特的减数分裂方式,以及 B 染色体的起源进化,与宿主及其基因组的相互作用等。事实上,对于 B 染色体的本质还远远没有阐明,其存在也可能并不完全是寄生的方式,有时可能也会对宿主产生良好的适应意义。

第五章介绍单个基因或小规模的基因重复,以及这些基因在基因组中演变与进化的过程和机制,最后以动物发育重要相关基因 *Hox* 家族为例,强调了基因重复在功能多样化过程中的重要作用。基因重复是生物进化中新遗传特征起源的重要过程,事实上目前对此问题的研究比这里的简要介绍还要广泛而深刻得多,有兴趣的读者可以跟踪最新

的相关文献。

第六章为研究基因组重复的两位著名科学家写就，他们是比利时的 Yves Van de Peer 和德国的 Axel Meyer。本章介绍了大规模基因重复和古老的基因组重复，以及这些大规模重复的机制（如多倍化和大片段重复）和脊椎动物中著名的一轮和两轮基因组重复学说，硬骨鱼类里的第三轮重复学说；最后讨论大规模重复后基因的保持机制和对物种形成的影响。

第七章专门描述植物中多倍体的物种分布、形成和维持机制，对植物细胞、有机体和基因组的影响。

第八章详细介绍动物中的多倍体类群和现象。在介绍了识别动物多倍体的研究方法和多倍化对动物体的影响后，又分两部分内容分别详细列举了脊椎动物和无脊椎动物中的多倍体类群，是动物多倍化研究里不可多得的信息来源。

第九章讨论的问题是日前基因组研究领域里的热门和主流方向，由 Alan Filipski 和 Sudhir Kumar 两位著名分子进化学家写就。本章介绍了真核细胞的比较基因组学，覆盖历史、概念、研究方法各类真核生物的基因组结构特征和比较结果，包括真菌（酵母）、原生动物、线虫和果蝇、植物（拟南芥和水稻）、大、小鼠和人类等最为重要的几类模式生物。这一章对急于了解进化基因组学的学生和初学人员来说，是非常重要的速成资料。

第十章介绍原核生物的比较基因组学：列举了原核生物测序的重大事件；讨论了一些重要概念和理论问题，如基因的水平转移和最小基因组概念等；在其小结中还涉及了生物恐怖问题。

第十一章的第一部分，Ryan Gregory 博士回顾了进化理论的发展，介绍了宏观进化理论的背景和框架，试图整合基因组学和宏观进化理论。本章的第二部分讨论了许多深刻的进化问题，如细胞的起源、性别的进化、真核和多细胞生物的起源、免疫的进化、脊椎动物的进化和人类基因组中的一些特征。

作者设计本书时，充分考虑了对基因组进化研究的全景介绍，对历史和基本概念的介绍和梳理，对每个领域各时期文献的综述和列举，并在每一章后面都做了小结和相关领域的展望。这样的处理使得全书比较通俗易懂，只要具备基本的生物学和遗传学知识就基本可以读懂。因此，正如编者所言，这是一本特别适合那些想了解或进入进化基因组学领域的研究生和博士后的书。但同时，由于该书综述了各个研究方面，列举了大量文献，因而即便是对于基因组学领域的专业研究人员和科学家也会是一本很好的参考书。

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2006 年 10 月

## 前言：基因组进化研究的进化

人们常说前言是一本书中最重要的部分。前言虽短，但前言难写这一事实却令我惶恐，让我倍感紧张。一个人如何在短短几页纸上把握（或整合）像这样一本涉及那么多人、那么多课题的书？我心中唯有的出路就是遵循那个古老的格言：人应当写自己最熟知的东西。基于此，我最好就用生物学术语来介绍这本书了。

这卷书的中心主题是，基因组代表着生物组织的一个特异的合理层次，有着其内在的特质和独特的进化历史。关于基因组的书本身也与生物个体一样，不时会经历难以预料的进化。到底什么是在编辑，是不是就是一个“智力选择（intellectual selection）”的过程，即作者尽情发表议论，而编辑在无情地取舍或修改？就像大自然中的生物一样，这本书的进化也涉及到了进化的各种健康力量，如形态学（长度）的限制，各部分间的必要协调，来自不同生物类群的数据整合，不同学科的“水平转移（horizontal transfer）”和概念“化用（exaptation）”，以及一些突发的偶然历史事件。

任何东西的进化，无论是活的还是文字性的，都是作用于数个组织层次的基本规律和特殊历史事件的结合。这本书在诞生过程中也发生了一些曲折的特殊事件。2002年，我到华盛顿特区参加会议，我的朋友兼同事 Grace Wyngaard 友好地接待了我。她的丈夫 Roy McDiarmid 是 Smithsonian 研究院爬行动物学的高级馆员。在那次会议上还碰到了 Academic 出版社的高级编辑 Chuck Crumly，他曾是爬行动物学家，是 Roy 的老朋友。通过这层关系，Chuck 找到我，说是要为 Academic 出版社出版一本有关基因组进化的书。

由于缺乏比较的数据，我只能大致说说这本书后来历史发展的特别事件：一个编辑新手设法组织了一个全明星的作者队伍并签订一个出版合同；最初的出版商被另一家公司吞并；接着出版队伍中又发生了一系列的出出进进（包括 Chuck Crumly 的离开）；一些原本答应参与编写的作者最终又不能参与；章节清单改来改去，一些著名的人物慷慨地同意参与修订；最终一本承载着两年那个午餐讨论的基本内容的新书成形了。

现在这本书终于付梓出版了，是考虑它的生态学和形态学的时候了，也即它所应处的生态位以及在这个生态位中采取的适应策略。

我的体会是，基因组生物学的原始文献并不那么易于掌握。在自己的专业领域中追踪发展趋势已是一个重大挑战，要想全面掌握基因组进化的全貌几乎是不可能的。横亘在研究不同基因组学问题或不同生物类群的学者之间的鸿沟依然是一如既往的宽广，而在生命科学中不同分支的隔阂似乎还在变得更大。这可能是理解基因组进化的背景和重要性的一个主要障碍，特别是对于那些初学者而言。

这本书中的各章节旨在对基因组学各主要领域的基本概念、历史、现状和展望提供全面的介绍。这些概念和历史常常由于不断涌现的新发现主导了话题而被忽视。总的说来，这本书主要是给那些正在成长的“基因组一代”看的，包括高年级研究生，博士后和年轻的教师。当然，对于那些相关领域的专家也是有用的。明确地讲，这本书是为那

些正在或将要塑造基因组生物学未来的人所写的。因此，它为各种眼花缭乱的关于基因组进化的文献提供了一个索引地图，在不同学科之间架设桥梁，更为重要的是呈献了基因组进化研究的全貌图景。在一些情况下，一些章节的主题还从未有过综述，因此我们设法阐述得详尽些；另外一些主题可能每个月都会有相关的综述，但可能不会像本书一样给出了广阔的背景知识。

所有这些都意味着这本书不是零星地收集几件琐事。本书也不是一本包罗万象的针对本科生的教科书，它需要扎实的生物学和遗传学背景知识来理解大部分的章节。当然，这也不是一本针对专家的高度专业化的论述。我们通过将学科专业化名词减到最少和不可避免时设法解释的方法，使所有拥有扎实基础生物学知识的读者都应该看得懂大部分章节。一言以蔽之，这是一本当我刚刚成为一个基因组进化专业的学生时所期望拥有的书。

虽然不同的章节为不同的作者写就，每一章节也可以独立成文，但我们保持了书的前后完整性，而不是一堆不相干的综述论文集。本书一开始讨论基因组大小的进化（第一、二章），这是一个自双螺旋被揭示以来就存在的谜题。紧接其后的是关于基因组寄生序列的讨论，首先是转座子（第三章），其次是 B 染色体（第四章）。第五章介绍单个基因的重复，第六章关于古老的大片段或整个基因组的重复，第七、八章则谈论近期染色体组的重复。随后的两章分别处理真核生物和原核生物的比较基因组测序，同时包含了这两类生物基因组结构和进化特征的信息（第九、十章）。最后，所有得自这些领域的新观点被放到了第十一章的进化理论背景之中。在这里，我们尽最大努力进行整合，在进化光谱的两极之间，即从亚基因组因子的研究到古生物学家提出的宏观进化理论之间架起桥梁。

正如 Stephen Jay Gould 在他最后一本关于进化理论的大卷本中指出的那样，“一本书产出的时间尺度如果与用生态学时间衡量的发现步伐相比，就必须用地质时间来标定”。这种进化速率的不一致在基因组科学中尤为严重，在这一领域中重大发现正在加速进行。基因组生物学发展如此之迅速，以至于当我们在输入这些文字时，我们都能感觉到我们所呈现给读者的可能不是最新的综述。此外，也不是所有现有的信息都能包容在这样一本长度有限的书中。最终的结果是，这些章节只是快速发展中的广泛课题的一个缩影或素描。尽管如此，虽然在我们挺进 21 世纪的过程中新的信息仍在不断涌现，这本书所描绘的历史和概念构架，对已有文献的指引，以及在学科间架起的桥梁，都会在相当一段时间内有用。事实上，本书的目的之一也就是希望通过基因组生物学现在和将来激动人心的研究内容来勾勒出本学科未来的发展方向；同时激发年轻的学者去追寻他们自己崭新的研究道路。

这本书的问世凝集了许多人的勇气、支持和辛苦的工作。对很多人，如果我忘了将你们列举致谢，我想在这里首先向你们道歉。相信我，我对所有人都充满感激之情。

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我感谢我亲人的爱、慷慨和鼓励, 以及你们所有的一切。包括我各方父母, Bob 和 Marilyn Gregory, Michele Davis 和 Frank Brewster, 以及 Steve 和 Carol Adamowicz, 我最持久和最亲近的老朋友、我的弟弟 Sean Gregory。最后, 我最特别的感谢要给予我美好的伴侣和朋友、顾问和照顾者、知己和志同道合的人: Sarah Adamowicz, 对你所作的一切再次表示衷心地感谢。

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T. Ryan Gregory  
英国伦敦  
2004 年夏

(王文 译)

## 作者简介

T. Ryan Gregory 博士于 1997 年在加拿大安大略省汉密尔顿城的 McMaster 大学获得生物学学士学位，2002 年在安大略省的 Guelph 大学获得进化生物学和动物学博士学位。他曾获得了好几项奖学金，2003 年获得了由加拿大自然科学与工程研究委员会颁发的加拿大著名的 Howard Alper 奖。在准备本书的过程中，他是美国自然历史博物馆和英国自然历史博物馆的博士后研究人员。

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## PREFACE: THE EVOLUTION OF *THE EVOLUTION OF THE GENOME*

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It has been said that the preface is the most important part of a book, because even the reviewers will read it. That strikes me as a lot of pressure to put on such a small fraction of a book, made no less disconcerting by the fact that the preface can actually be rather challenging to write. How does one encapsulate, in only a few pages, a book that covers (and integrates) as many topics, involved the input of as many people, and has taken as much work to prepare as this one? The only strategy that comes to mind is to follow the old adage that one should stick to writing what one knows best. As such, it seems reasonable (and actually quite appropriate) to discuss this book in biological terms.

A central theme of this volume is that genomes represent a distinct and legitimate level of biological organization, with their own inherent properties and unique evolutionary histories. Books about genomes, too, are organized entities that evolve in sometimes unpredictable ways, and are subject to the same general processes as biological individuals. What is editing, really, but an example of “intellectual selection,” whereby the author proposes and the editor disposes (or at least ruthlessly modifies)? As with life at large, the evolution of this book also involved healthy doses of morphological constraint (especially in regard to length), the necessary coordination of parts, hybridization of data from the study of very different taxonomic groups, horizontal transfer and exaptation of concepts among disciplines, and more than a little quirky historical contingency.

The evolution of any entity, living or literary, is a combination of general principles (acting at several levels of organization) and unique historical particulars. The convoluted particulars of this book’s genesis are as follows. In 2002, I ventured to Washington, DC to attend a conference. While there, I was kindly hosted by my friend and colleague Grace Wyngaard, whose husband, Roy McDiarmid, is a curator of herpetology at the Smithsonian Institution. Also at the conference was

Chuck Crumly, then a senior editor at Academic Press, who had also trained as a herpetologist and was an old acquaintance of Roy's. Through this connection, Chuck approached me with the notion of preparing a book on genome evolution for Academic Press.

Lacking any comparative data, I can only speculate as to how typical the rest of the book's history is: Rookie editorial hopeful manages to assemble an all-star list of authors and gets a book contract; original publisher is phagocytosed by another company; there ensues a chaotic series of comings and goings on the publishing team involved with the book (including the departure of Chuck Crumly); some authors who planned to contribute are unable to; the chapter list is juggled and reshuffled, and other equally stellar contributors graciously agree to join the revised project; and in the end, a book emerges that bears at least a modest resemblance to the one discussed over a lunchtime meeting more than two years earlier.

Now that the book has come into being, it is worthwhile to consider some aspects of its ecology and morphology—that is to say, the niche it is meant to occupy and the ways in which it is adapted to do so.

Speaking from experience, I can attest that the primary literature of genome biology is, shall we say, less than readily accessible. It can be a significant challenge to follow developments in one's own specialized subdiscipline, and a near impossibility to obtain a broad view of genome evolution at large. The chasms separating researchers working on different genomic questions or with different taxa are as wide as ever, and those dividing the various branches of the life sciences seem to be getting wider. This can be a major barrier to understanding the context and importance of genome evolution, a problem that is particularly acute for newcomers.

The chapters in this book are meant to provide comprehensive summaries of the underlying concepts, histories, current statuses, and future prospects of the major fields of genomic inquiry. Too often, these conceptual and historical underpinnings are overlooked as new discoveries come to dominate discussions of these topics. Overall, this book is aimed at the up-and-coming "genome generation"—advanced graduate students, postdocs, and young faculty members—although it should also serve as a valuable resource for existing experts in these and related fields. Put explicitly, it is written for the people who are, and will be, shaping the future of genome biology. It therefore provides a map to the otherwise bewildering maze of literature on genome evolution, seeks to build much-needed bridges between divergent disciplines, and, perhaps most importantly, stresses the big picture. In some cases, the subject of a given chapter has never been reviewed before, and, as such, is treated as comprehensively as possible. In others, the subject could be (and in some cases is) reviewed every few months, though seldom in the broad context emphasized here.

All of this means that this book also is *not* several things. Notably, it is not a comprehensive textbook for undergraduates, meaning that a strong basic background

in biology and genetics will be required to get the most out of these chapters. However, neither is it a typical collection of highly technical reviews accessible only to other specialists. By keeping discipline-specific jargon to a minimum (and making all attempts to define it when unavoidable), the chapters provided here are meant to be accessible to anyone with only a strong basic biological background. In a phrase, this is the book that I wish had been available when I was first starting out as a student of genome evolution.

Although the various chapters have been written by several different authors and each can stand on its own, the book is designed as a cohesive whole rather than a collection of independent reviews. The volume begins with a discussion of the evolution of genome size (Chapters 1 and 2), which has remained a puzzle in genome biology since before the elucidation of the double helix 50 years ago (and, not coincidentally, is my own primary subject of study). This is followed by a discussion of genomic parasites, first in the form of transposable elements (Chapter 3), and then of B chromosomes (Chapter 4). Next comes a series of chapters dealing with duplications—of individual genes (Chapter 5), of large fragments and entire genomes in the ancient past (Chapter 6), and of whole chromosome sets in more recent times (Chapters 7 and 8). The following two chapters treat the topics of comparative genome sequencing in eukaryotes and prokaryotes (Chapters 9 and 10, respectively), and include information on genome structure and evolution in the two groups. Finally, the new insights derived from genomic analyses in all these areas are placed in the context of evolutionary theory (Chapter 11). Here the policy of integration is taken to the extreme by drawing links between opposite ends of the evolutionary spectrum, from the study of sub-genomic elements to the macroevolutionary theory developed by paleontologists.

As Stephen Jay Gould noted in his last tome on evolutionary theory, “[a] book’s timescale of production must be labeled as geological compared with a pace of discovery that can only be measured in ecological time.” This disconnect in evolutionary rates is especially acute in genomic science, where major discoveries are being made at an ever-accelerating tempo. In fact, the field of genome biology is moving so quickly that even looking over our shoulders as we typed would not guarantee a fully up-to-date review for the reader. Nor can all of the information presently available be treated in complete detail within the constraints of a single book. The net result is that these chapters are, of necessity, both snapshots and sketches of dynamic and wide-ranging subjects. However, even though much new information continues to accrue as we move deeper into the 21<sup>st</sup> century, the basic historical and conceptual background, the inroads to the existing literature, and the cross-disciplinary bridges provided in these chapters should remain useful for some time. In fact, one of the goals of the book is to help shape the future development of genome biology by highlighting exciting current and potential research and, hopefully, by stimulating young researchers to pursue their own novel avenues of investigation.

A book like this comes to exist only through the encouragement, support, and hard work of many people. So many, in fact, that it is probably prudent to simply apologize in advance to anyone I may fail to list here by name. Believe me, you are appreciated nonetheless.

To start, let me extend sincere thanks to Beth Callaway, David Cella, Bonnie Falk, Sarah Hager, and especially Chuck Crumly and Kelly Sonnack, along with everyone else at Academic Press/Elsevier and Graphic World Publishing Services who helped to guide this project from a rough idea concocted over mediocre Chinese food to a detailed, comprehensive, accessible collection of chapters that makes quite a satisfying thud when dropped on a desk.

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I owe an enormous debt to the various authors who contributed to this volume. Their hard work, dedication, and expertise have, I believe, made this book something of which we can all be very proud. Thank you!

To my various sets of parents, Bob and Marilyn Gregory, Michele Davis and Frank Brewster, and Steve and Carol Adamowicz, and to my oldest and closest friend (who also happens to be my younger brother), Sean Gregory: thank you for your love, generosity, encouragement, and, well—thank you for everything. And finally, the biggest thank you of all to my wonderful partner and friend, counselor and caretaker, confidant and fellow explorer, Sarah Adamowicz: thank you so much—again, for everything.

I dedicate this book with love to all the members of my family, genetic and otherwise.

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