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Plant Cell Biology
From Astronomy to Zoology

植物细胞生物学
从天文学到动物学

Randy Wayne

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Edited by

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Dedicated to President John F. Kennedy
for inspiring my generation to be courageous in the pursuit of science

谨以此书献给约翰·F. 肯尼迪总统
他给予我们这一代人追求科学的勇气

导　读

细胞是一切生物有机体的基本结构和功能单位。细胞生物学是研究细胞结构及其生命活动规律的学科。虽然生物化学过程的某些环节可以在非细胞体系中进行，但是有机体正常的、有规律的生命活动必须要以细胞作为基本单位才能实现与完成，从这一点上讲，没有细胞就没有生命，生命是细胞特有的属性。因此，对细胞生命活动基本规律的研究是一切生命科学的重要基础。细胞生物学、生物化学和遗传学是生命科学的三大基础学科。随着分子生物学的迅猛发展，人们现在可以在分子、超微结构、细胞、器官和个体等不同水平上研究生命活动的规律。

在种类繁多、浩如烟海的细胞世界中，根据其进化地位、结构的复杂程度、遗传装置的类型与主要生命活动的方式，可以将细胞分为原核细胞（prokaryotic cell）与真核细胞（eukaryotic cell）两大类。原核细胞没有典型的细胞核，即没有核膜将它的遗传物质与细胞质分隔开，也没有内膜系统。真核细胞与原核细胞最根本的区别有两点：其一是有了细胞膜系统的分化与演变；其二是遗传信息量与遗传装置的扩增与复杂化。真核细胞在进化过程中，演化出了动物细胞和植物细胞，两者有许多共同的特性，但又有明显的区别：即植物细胞有细胞壁、液泡和质体。植物细胞壁如同一个庭院或庄园的围墙，为植物细胞提供了一个保护性的外围屏障，用相对坚固的结构包围着内部的原生质体，起着重要的支撑和保护作用。成熟的植物细胞具有一个巨大的中央液泡，它占据细胞总体积90%以上，是植物细胞区别于动物细胞的显著特征之一。质体的存在是植物细胞区别于动物细胞的最重要特征之一。植物细胞中有着多种类型的质体，其中最重要的是叶绿体，它所进行的光合作用为所有生物体的生存提供了有机物质的基础，也是植物自养的基础。

由于种种原因，国内外细胞生物学的教材很多，但内容大都是以动物细胞为主，很少有以植物细胞为主要素材和论述对象的教材。国内只有郑国锠先生主编的《细胞生物学》介绍了植物细胞的有关知识，但没有一本植物细胞生物学方面的专门教材。近年来，随着拟南芥和水稻等模式植物基因组测序完成，结合分子生物学和激光共聚焦显微镜等先进技术，有关植物细胞的结构、功能、生长、发育、进化和起源等都积累了大量数据和结果。我国作为农业大国在植物科学，特别是作物科学研究方面投入了大量的研究经费，也取得了突出的成就，使我国植物科学研究与世界先进水平迅速缩小。另一方面，从事植物科学研究的队伍迅速壮大，学习植物学科的学生也逐年增加。遗憾的是，国内还没有专门的植物细胞生物学教材。

美国康奈尔大学植物生物学系的 Randy Wayne 教授主编的《植物细胞生物学》是植物细胞生物学领域的最新专著，是 Randy Wayne 教授 20 多年从事植物细胞生物学教学和科研的结晶。在过去的 20 多年里，他从参与这门课程的教师和学生的问题与见解中将这本教材的内容不断发展完善，几次改名，反复修改。这本教材不仅将遗传学、生物化学、进化、数学、物理学和化学融入植物细胞生物学，同时还把植物解剖学、植物

生理学、植物生长和发育、植物分类学、植物生物化学、植物分子生物学等课程与植物细胞生物学有机地联系起来。Randy Wayne 教授渊博的知识使本书对植物细胞的介绍不再是将细胞描述成死的东西，而是运用数学、物理学、哲学等方面的知识阐明细胞的特性，有助于学生了解细胞的性质，有助于学生对细胞的起源、生命的起源产生兴趣和好奇，有助于学生了解细胞内各细胞器之间、细胞与细胞之间、细胞与环境之间每时每刻所进行的物质、能量和信息交换所遵循的原理及规律。这从原著的副标题"从天文学到动物学"（From Astronomy to Zoology，注一）就可以窥见其所涉及知识面之宽广。

本书共 20 章。其中第 1 章简要介绍了细胞、细胞的组成、细胞的大小、细胞生物学及人们对生命的认识过程等基本知识。使学生能根据这些知识了解"什么是生命？生命的基本单位是什么?"。第 2～11、13、14、16、17 和 20 章依次论述了细胞质膜、胞间连丝、内质网、过氧化物体、高尔基体、液泡、内膜系统内的运动、细胞质的结构、激动蛋白及微丝介导的过程、微管蛋白和微管介导的过程、叶绿体、线粒体、细胞核和细胞外基质。这 15 章是该书的主要部分，详细地论述了植物细胞结构研究和发现的历史、如何分离这些细胞器及结构、它们的化学组成、起源及其功能，最后进行总结并列出有关的思考题。使学生能够全面、系统地了解植物细胞生物学基本知识和基本概念；了解植物细胞生物学研究的基本思路和方法；了解细胞内各细胞器之间既有共同点，又在结构、组成及分工等方面不同，细胞内各细胞器之间每时每刻所进行的物质、能量和信息交换使细胞能够进行分裂、分化和生长。第 19 章讨论了植物细胞分裂。有丝分裂过程即一个细胞分成两个细胞，主要介绍了细胞核分裂的过程及其机制，也描述了胞质分裂的过程及其所涉及的主要事件。有助于学生了解一个种子是如何长成参天大树等细胞数目的增加及细胞分化的过程及其机制。第 15 和 18 章讨论细胞器及生命的起源这样一些最基本也是最难回答的问题。真核细胞含有许多细胞器，其中内质网、高尔基体、液泡和细胞核来源于内陷的质膜，而叶绿体和线粒体则来自于被细胞内吞的细菌，但过氧化物酶体和中心粒的来源尚不清楚。对生命起源这种尚未解决的难题作者也进行了论述并提出了自己的观念，而且是从宇宙的起源、时间的概念、哲学、地球化学、达尔文进化论、生物多样性等多学科、多角度来讨论生命的起源。有助于学生根据这些知识对细胞的起源、生命的起源产生兴趣和好奇，并自己去观察和思考。第 12 章讨论了细胞信号转导。主要讨论环境刺激、受体、外界刺激通过受体转化成胞内信号的机制、胞内信号系统如何介导生理生化响应等的过程及机理。这些知识有助于学生了解植物如何对环境做出的适应性反应，从而全面了解细胞与细胞之间、细胞与环境之间每时每刻所进行物质、能量和信息交换所遵循的原理及规律。

该书的第一个特点是以植物细胞的结构和功能为重点，编者试图以最好的例子来说明一个过程，选用了大量植物细胞生物学最原始的图片和数据，突出了现代植物细胞生物学的基本内容，由表及里、由结构到功能、按自然的内在联系依次介绍。使读者对植物细胞的主要结构和功能、两者之间的复杂关系和作用，以及细胞器和生命的起源与演化等有一个系统而全面的了解和认识。

该书的第二个特点是编者试图重新建立曾经在数学、天文学、物理学、化学、地质学、哲学和生物学之间存在的联系。本书运用了大量的数学来对细胞过程进行研究，包括膜运输、光合作用和呼吸作用，目的是为了能够探索这些过程和发生在这些过程中不

同形式能量之间的转换。运用数学来研究细胞生长、染色体运动、膜转运，目的是能够假设和评估发生在这些过程中的可能的机制，以及这些过程和推动这些过程的生物能量之间的相互关系。使读者能从多维视角、多学科观察植物细胞，了解有机体内的细胞与其他细胞之间的相互作用，细胞与环境之间的相互作用，细胞的起源和进化。

该书的第三个特点是不仅描述了现代植物细胞生物学的新成果，还对这些成果背后的原始方法及研究思路进行描述，目的是让读者熟悉在科学上伟大的发现者，学习他们做科学的方法，学习或了解科学家是怎么选择和提出问题的，又是如何解决问题的。该书特别推崇利用相对低技术含量的定量和观测方法在细胞生物学做出重大发现的科学家们，强调达到同样目的用最简短、最经济和最科学的方法就是最好的方法，而不提倡简单地利用昂贵的仪器去重复同样的实验。

该书附有与植物细胞生物学有关的 SI 单位、常量、变量和几何公式；一个细胞生物学家的非牛顿物理观；总横力的计算及其与应力的关系；利用普通光学显微镜、相差显微镜和荧光显微镜观察植物细胞、细胞分裂、质壁分离、细胞极性及如何测定细胞膜透性、细胞质运动等最基本的植物细胞生物学实验。还附有专业名词索引。这些附件对于读者学习和理解植物细胞生物学有很大帮助。

该书适合作为植物科学研究生课程的教科书或参考书，也适合作为本科生的参考书。对于从事植物学、植物生理学、植物遗传育种、植物发育生物学、植物分子生物学和植物系统学的教学和科研人员都具有重要参考价值。

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山东师范大学生命科学学院
2010 年 7 月　于济南

前　言

这本书实际上是我在康奈尔大学讲授植物细胞学的讲义。迄今为止，这份讲稿已经有过好几个标题了，包括："Cell La Vie"（注二），"The Book Formerly Known as Cell La Vie"，"Molecular Theology of the Cell"，"Know Thy Cell"（with apologies to Socrates，注三），"Cell This Book"（with apologies to Abbie Hoffman，注四），"Impressionistic Plant Cell Biology"。我想介绍一下这门课程。这是一门学期比较长的课程，主要针对本科生和研究生。因为大学生物学要求学生主修遗传学、生物化学和进化，还要学习 1 年的数学和物理学，以及 2 年的化学。我尽量在教学中融入这些学科的知识。另外，许多学生也学习植物解剖学、植物生理学、植物生长和发育、植物分类学、植物生物化学、植物分子生物学、还有各种各样的以后缀"组学"（"-omics"）结尾的课程；我尽量把这些课程与植物细胞生物学联系起来。对于没有植物学基础的人而言，Mauseth (2009)、Taiz 和 Zeiger (2006) 编著的两本书是非常好的人门读物。

在过去的 20 年里，许多内容已经从参与这门课程的师生的问题和见解中不断发展完善。世界各地的细胞生物学家所做的富有想象力和深刻见解的研究引发了学生的兴趣。

我的理念是，大学所教授的学科领域之间并非泾渭分明、水火不容，这种壁垒仅仅存在于教师和研究人员的意识中。我希望我的学生没有把植物细胞生物学看成一个孤立的学科领域，而是作为人类探索科学各个方面的敲门砖。我教授这门课程的目标之一是试图重新建立曾经在数学、天文学、物理学、化学、地质学、哲学和生物学之间存在的联系，这是我个人的尝试，我深知这不是一件容易的事情，需要持之以恒、不断努力。即使如此，我将尽我所能为我的学生提供学习动力和资源，以便使这些不同学科有机地结合在一起，从而使每个学生从不同的研究领域编织成一个带有个人色彩的细胞"十字绣"。

考虑到所有活的真核细胞是基本相似的（Quekett，1852，1854；Huxley，1893），我会在课程中讨论动物和植物细胞。虽然举的例子更多偏向于植物（因为这是植物细胞生物学课程），但我力图以最好的例子来说明一个过程，有时候最好的例子来自动物细胞。我采用的是 August Krogh (1929) 的方法；也就是说，在自然生物宝库中存在着多种多样的生物，你总能找到一种生物去阐明一个原理。我试图以一种平衡的方式来讲述课程，不去强调任何一种植物、细胞器、分子或技术，而是尽力覆盖到植物细胞生物学的各个方面。但是，我也意识到现在植物细胞生物学的大部分文章正在使用几种模式生物和"组学"技术。虽然学生在其他课程中可以了解利用这些方法取得的成就，但是，我要告诉他们还有许多其他方法。

毕达哥拉斯（Pythagoras，古希腊哲学家、数学家）相信数学，我认为数学有助于了解细胞的性质。在授课时，我运用数学来帮助叙述细胞的数量关系，可以帮助学生了解一些很容易测量的参数（Hobson，1923；Whitehead，1925；Hardy，1940；Synge， 1951，1970；Feynman，1965；Schrödinger，1996）。例如，一个长方形的面积是难以测量的，但是如果知道了它的长度和宽度，那么面积就是长乘宽的积，这样就能从容易衡量的数据计算出面积。同样，圆周或圆的面积也是比较难测量的。但是，如果测量了直径，用直径乘以 π 或是直径的平方乘以 $\pi/4$，就可以很容易分别获得周长和面积。同样，如果你懂得三角和正切的定义，可以轻松地用容易测量的数量来估计树的高度。

物理学家 Hans Bethe 在康奈尔大学纪念费米（Enricho Fermi）发现链式反应 50 周年会议上讲述的故事深深地影响了我的教学。Bethe 谈到他的研究生导师 Arnold Sommerfeld 和他的博士后合作导师费米之间的差异。他说在原子物理学领域，Sommerfeld 在创造数学理论来描述现有的数据方面是一个天才，但是他的技能依赖已知的数据。而费米不同，他能提出一种理论，即使没有明显的相关数据。他会从基本原理估计数据，例如当第一颗原子弹在阿拉莫戈多爆炸时，他通过测量小纸片落地的距离就可以估计第一个原子弹的当量。我们知道冲击波强度和爆炸距离的平方成反比，费米把原子弹的爆炸和小纸片落地联系了起来。在爆炸后几秒内，他计算出了爆炸当量大约是 20 千吨当量，这个结果和用昂贵的仪器记录的结果类似（Fermi，1954；Lamont，1965）。

为了培养学生估计他们不知道的事情，费米问道："在洛杉矶有多少钢琴调音师？"当看到学生毫无头绪时，他会说："你们可以用基本原理来估计一下钢琴调音师的人数！例如，在洛杉矶有多少人？如果有一百万？这些人中有钢琴的比例是多少？如果是 5%，那么在洛杉矶就有 50 000 架钢琴。那么钢琴需要多长时间调一次？如果大约一年一次，那么这 50 000 架钢琴在一年内都需要调试。然后就是一个钢琴调音师一天能调多少架钢琴？如果是 3 架，那么一个钢琴调音师一年内必须花费 16 667 天。但是既然一年内没有那么多天，他（或她）一年内可能只能工作 250 天，所以在洛杉矶就必须有 67 个钢琴调音师。"

我的学生运用数学来对细胞过程进行研究，包括膜运输、光合作用和呼吸作用，目的是为了能够探索这些过程和发生在这些过程中不同形式能量之间的转换。我的学生运用数学来研究细胞生长、染色体运动、膜转运，目的是能够假设和评估发生在这些过程中的可能的机制，以及这些过程和推动这些过程的生物能量事件之间的相互关系。轻松地运用数字让学生更容易理解、完善和发展理论。"正如希腊单词［theory］所暗示的，理论是真正看到的东西——敏锐的洞察力来自于健康的视力"（Adams and Whicher，1949）。

我的学生能够利用数学把看似无关的过程联系起来，尝试根据基本原理分析所有的结论。他们也学会了根据基本原理进行预测。学生必须明确他们正在考虑的是事实；他们正在考虑的是事实之间的关系；并且他们正在假设。这为研究提供了一个好的切入点，因为事实必须加以完善，假设必须加以验证（East，1923）。

除非必要，否则我不会在上课时介绍太多术语，但是我会解释每个术语的来源。有些专业术语是基本的，因为对科学问题的精确沟通需要这些专业术语，就像描述爱与美的术语一样。然而，有些专业术语因为有一个冠冕堂皇的名称似乎很容易理解，但是它们的创造掩饰了我们的无知，进而妨碍人们的深入探究（Locke，1824；Hayakawa，1941；Rapoport，1975）。在歌德（1808）《浮士德》的第一部分，Mephistopheles 说："在概念的解释方面，一个字就可以产生完全不同的理解。"弗兰西斯·培根（1620）把

这个现象称为“市场假象”(注五)。很多时候当我们用希腊语或是拉丁语回答了一个问题，我们就认为自己是伟大的思想家。例如，如果有人问我：“为什么叶子是绿色的?”我会立即回答：“因为它们有叶绿素。”提问的人很满意并且说：“哦。”这个谈话结束了。但是，叶绿素在希腊语里是绿叶的意思，这样，我用重复这个问题的方式回答了这个问题。我等于在说“叶子是绿色的，因为叶子是绿色的。”，所以根本没有回答这个问题。这就像是我从文章中背诵了一句话，这句话我没有思考只是记住了。但是，我刚才用希腊语回答的问题，并且是具有权威的——所以这是一个科学的回答。

在《人类理解论》(*An Essay Concerning Human Understanding*) 一书中，John Locke (1824) 告诫说人们经常以一种不理智的方式运用言论。他写道：

他并不比前面提到的印度人好多少，那个人说世界被一只大象支撑着，有人问他大象站在什么东西上，他的回答是一只大乌龟。但当进一步再问他什么支撑着这只乌龟，回答是他不知道的某种东西。这就像在其他情形下一样，我们所说的话没有明确的思路，我们像个孩子似地谈论；当有人问他们不知道的事情是什么时，他们很容易给出满意的回答，那是某某；说这样的话的人，不论是孩子还是成年人，其实是什么都不知道的人。他们以为自己完全理解了，并且毫无边际的夸夸其谈。

有时候有些术语出现后就会变成这个领域的口号，有时它们是由于政治原因、经济原因而产生的，或是把荣誉从发现某一事物的人转给重新命名这个事物的人 (Agre et al., 1995)。Joseph Fruton (1992) 叙述 (和翻译) 了巴尔扎克的名著《驴皮记》中与著名化学家的一段谈话：

看到 Japhet 坐在椅子上检查沉淀，Planchette 说“嗯，我的老朋友，研究进展怎么样啊?”

“一切照旧，没有新东西。在此期间该科学院承认水杨苷 (salicine) 的存在。但水杨苷、天冬酰胺、马钱子碱和洋地黄毒苷并不是新发现。”

Raphael 说，“如果一个人不能提出新的事物，那就意味着你被迫创造新的名词。”

“年轻人，那确实是真实的”。

我用历史的方法教授植物细胞生物学，“不仅教他们果实，还要教他们孕育果实的树以及种植这些树的人”(Lenard, 1906)。这样的方法有助于学生们理解术语的来源和含义；有助于他们捕获发现的那一激动人心时刻；有助于阐明在科学领域我们如何知道我们所知道的事情；这强调了人类思想的统一性和连续性 (Haldane, 1985)。我想让我的学生熟悉在科学上的伟大的创新者，学习他们做科学的方法 (Wayne and Staves, 1998, 2008)。我想让我的学生学习或了解科学家是怎么选择和提出问题的，他们是如何解决问题的。我不想让我的学生们只知道结果，然后在考试时将这些结果重新写在答题纸上 (Szent-Györgyi, 1964; Farber, 1969)。我不想让我的学生们变成仅能在另一生物体重复别人工作的科学家。我想让我的学生们可以像雅典公民一样，按照伯克里克的说法，“不要模仿——而要成为其他人的模范”。无论我的学生是否能变成专业的细胞生物学家，我都希望他们永远保持着对细胞生物学的爱好。也就是说，我希望我已经帮助他们变成“一个爱细胞生物学的人”和“一个喜欢细胞生物学的人”(Chargaff, 1986)，而不是变成一个无法识别一堆砖块和一栋大厦之间的差别的人 (Forscher, 1963)，不是销售“买”(buyology) 的人 (Wayne and Staves, 2008)，不是出售他 (或她) 学术

自由的人（Rabounski，2006；Apostol，2007）。

人们通常认为一门科学课程应该教授新的东西，但是我用 Erwin Chargaff（1986）讲述的一则有趣的轶事回答这个问题："德国皇帝威廉一世，俾斯麦的老皇帝，参观了波恩天文台并问主任：'奥，亲爱的阿尔格兰德，在星空中有什么新的吗？'主任迅速地回答：'陛下是否已经知道老的呢？'据说皇帝每次说起这个故事都会大笑。"

引自 R. John Ellis (1996)：

"考虑一个新问题的起源是有用的，这主要有两个原因：一是这具有指导意义；科学的历史提供给我们的是经过冷静思考的、可以让人相信的信息，这些信息是有关不能忽视的观察的重要性，尽管这些观察不适合当时的概念和理解；是有关横向思维的价值，以免让一些无关的现象掩盖的一般原理。其次，一旦一个新想法被普遍接受，往往有一种倾向，认为这一直是并且以后也是一个非常好的事情，但问题是，你却从来不需要它！"

历史的方法是必要的，用 George Palade（1963）的话说："历史的方法表明了在长期的一系列类似的探索中形成了近来的发现和现在的概念，当然，这种探索不会结束。"

我告诉我的学生无论是考虑老的观念还是新的观念，持怀疑态度是同样重要的。引自 Thomas Gold（1989）：

"因为科学中的新思路是新的东西，所以并不总是正确的。同样老的思路并不是因为它们是老的而总是错误的。每个科学家都需要有批评的态度，而且这种态度在对待老的观念和新的观念上应该相同。每当一种观念被全盘接受，与之相矛盾的新证据就会因为它不符合这种观念而被忽视，也就不被报道，那么该科学就会深陷泥沼——这在过去的历史上经常发生。"

为了强调科学家唯命是从的接受传统智慧的问题，Conrad H. Waddington（1977）提出缩写词 COWDUNG 以寓意优势群体的传统智慧（Conventional Wisdom of the Dominant Group）。

以一种历史的方式教授课程，我认识到 Thomas H. Huxley（1853）警告的重要性，他告诫人们："真理绝不是神仙下凡，无论人们多么健忘，历史永远是公正的，它不允许那些为探求真理曾经遭遇不幸的人们在过世后被遗忘"，"世人总是喜欢讨好富人，而从穷人那里带走他们最宠爱的东西。"的确，很难确定究竟是谁发现的（Djerassi and Hoffmann，2001）。我将尽其所能来对细胞生物学的历史有一个公平和精确的评价。

我的课程包括一部分实验，我的学生通过实验来获得个人对活细胞以及活细胞如何工作的认识（Hume，1748；Wilson，1952；Ramón y Cajal，1999）。Justus von Liebig（1840）这样描述实验课程的重要性：

"自然界用一种特殊的语言对我们说话，即以现象为语言；她总是回答我们提出的问题；这些问题是实验。实验是一种思想的表述：当某一现象通过实验得出与我们的想法相符的结果时，我们就更接近事实。而与之相反的结果表明问题是虚假的，观念是错误的。"

我的学生总是迫不及待的进入实验室，他们经常在晚上和周末使用显微镜拍摄显微照片。学期结束时，学生们来我家吃晚饭（我上课和做饭都有独到的方法），并把他们的最佳显微照片带上。晚饭后，他们选出 12 张最好的，并把这 12 张显微照片做成一个

日历。这些日历很精美，学生往往把多做的作为礼物送给别人。

Edgar Bright Wilson Jr. 于 1952 年在《科学研究导论》《*An Introduction to Scientific Research*》写到："不能为这样的事情找任何借口：即同样有效的做某一工作本来可以通过减少开支而却以昂贵的方式去做。"今天更要强调，在科学研究方面大学获得大量的钱用昂贵的技术去研究一些细胞生物学已经回答了的问题。但是，使用昂贵的技术往往阻碍了一个人做预备实验，但预备实验对于了解怎样做实验才可能产生有意义有价值的数据是必要的，而不仅仅是列举数据。遗憾的是，通过昂贵的技术产生的数据常常需要统计人员和计算机程序员，他们没有通过观察和测量来体验生活细胞，所以不能告诉科学家所列举的数据中哪些是有意义的。因此有可能造成区别有意义的科学和无意义的科学变得模糊。我用 John Synge (1951) 的文章《恶性循环》帮助我的学生们认识到有必要区别什么是根本，什么是派生。

相比之下，这本书强调了那些利用相对低技术含量的定量和观测的方法已经在细胞生物学上作出了重大发现的科学家们的重要性。但是，这些科学家们同样把他们的大脑、眼睛和双手看成是高度发达的、不可取代的科学仪器。我希望我的学生们能了解这些伟大的科学家。我让他们说出心目中 10 位最伟大的科学家的名字。然后我问他们是否读过这些科学家的原始文献。他们大多从来没有读过任何一个人的原始文献。这是一个耻辱，他们读了其他人的工作……但不是最好的。有趣的是，他们对一些著名作家的作品却百读不厌（例如莎士比亚、福克纳等）。

通常情况下，学生们所列出的最好的科学家写的书要么是给外行人写的，要么是自传（Wayne and Staves，1998)。甚至牛顿也为外行人写过一本书！我给我的学生们一些参考书目并鼓励他们熟悉自己喜爱科学家的第一手资料。我的课程和这本书的目的是使我的学生们在生命科学研究历程中得心应手。

我教授植物细胞生物学的目的不仅仅是帮助学生了解细胞及其细胞器如何把能量和物质转化成活的有机体并维持其生命活动的机制。我还希望通过本课程加深学生对生命价值、生命本质和生命美的理解，从而去探索涉及生命所有过程的机理及其意义。

感谢 Mark Staves 和我的家人，Michelle，Katherine，Zack，Beth，Scott，我的父母，姑姑和叔叔们，感谢他们多年来的支持。我还要感谢康奈尔大学的同事，洛杉矶马萨诸塞州大学、佐治亚州立大学和加州大学的同事们，特别是 Peter Hepler 和 Masashi Tazawa，他们教会我怎样看到一个活细胞的世界。

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（王宝山 译）

注　释

注一：From Astronomy to Zoology，即从 A-Z，有包罗万象，包括所有学科的意思。即作者在前言中提出的“尽量在教学中融入数学、物理、化学等学科”的思想。

注二：取自法语 C′est La Vie，意思是 This is the life。作者取这个名字，一语双关，包含了“This is the cell”和“Cell life”之意。

注三：取自苏格拉底的名言 Know Thy Self（所以作者开玩笑说向苏格拉底致歉），Know Thy Self 即 Know Yourself，也就是“自知之明”的意思。这里是 Know Your Cell 之意。

注四：Abbie Hoffman 是美国六十年代叛逆青年的代表性人物，雅皮士组织的创始人之一，电影《阿甘正传》里让阿甘上台来谈谈越战的人就是他。他在 1971 年出版了一本很有影响的书《Steal This Book》（这个书名本身就很叛逆，意思是让大家在书店里看到这本书，不要掏钱购买，把它偷走就行了。这导致很多书店一度拒绝这本书上架）；作者的“Cell This Book”显然是取了“Steal This Book”的谐音，所以作者说向 Abbie Hoffman 致歉。

注五：培根把扰乱我们心灵的假相和错误概念分为四类，即：族类假相、洞穴假相、市场假相和剧场假相。市场假相与语言有关，如果交流中，用语选择不当或者概念不清，就会造成偏见和错误。语言作为信息交流的工具，它所传递的不但可能有假信息，而且也可能由于受纳者在解读信息时误解了信息的含义，从而导致“市场假象”的产生。

Preface

This book is in essence the lectures I give in my plant cell biology course at Cornell University. Heretofore, the lecture notes have gone by various titles, including "Cell La Vie," "The Book Formerly Known as Cell La Vie," "Molecular Theology of the Cell," "Know Thy Cell" (with apologies to Socrates), "Cell This Book" (with apologies to Abbie Hoffman), and "Impressionistic Plant Cell Biology." I would like to take this opportunity to describe this course. It is a semester-long course for undergraduate and graduate students. Since the undergraduate biology majors are required to take genetics, biochemistry, and evolution as well as 1 year each of mathematics and physics, and 2 years of chemistry, I have done my best to integrate these disciplines into my teaching. Moreover, many of the students also take plant anatomy, plant physiology, plant growth and development, plant taxonomy, plant biochemistry, plant molecular biology, and a variety of courses that end with the suffix "-omics"; I have tried to show the connections between these courses and plant cell biology. Nonbotanists can find a good introduction to plant biology in Mauseth (2009) and Taiz and Zeiger (2006).

Much of the content has grown over the past 20 years from the questions and insights of the students and teaching assistants who have participated in the class. The students' interest has been sparked by the imaginative and insightful studies done by the worldwide community of cell biologists, which I had the honor of presenting.

I have taken the approach that real divisions do not exist between subject areas taught in a university, but only in the state of mind of the teachers and researchers. With this approach, I hope that my students do not see plant cell biology as an isolated subject area, but as an entrée into every aspect of human endeavor. One of the goals of my course is to try to reestablish the connections that once existed between mathematics, astronomy, physics, chemistry, geology, philosophy, and biology. It is my own personal attempt, and it is an ongoing process. Consequently, it is far from complete. Even so, I try to provide the motivation and resources for my students to weave together the threads of these disciplines to create their own personal tapestry of the cell from the various lines of research.

Recognizing the basic similarities between all living eukaryotic cells (Quekett, 1852, 1854; Huxley, 1893), I discuss both animal and plant cells in my course. Although the examples are biased toward plants (as they should be in a plant cell biology course), I try to present the best example to illustrate a process and sometimes the best examples are from animal cells. I take the approach used by August Krogh (1929); that is, there are many organisms in the treasure house of nature and if one respects this treasure, one can find an organism created to best illuminate each principle! I try to present my course in a balanced manner, covering all aspects of plant cell biology without emphasizing any one plant, organelle, molecule, or technique. I realize, however, that the majority of papers in plant cell biology today are using a few model organisms and "-omic" techniques. My students can learn about the successes gained though this approach in a multitude of other courses. I teach them that there are other approaches.

Pythagoras believed in the power of numbers, and I believe that the power of numbers is useful for understanding the nature of the cell. In my class, I apply the power of numbers to help relate quantities that one wishes to know to things that can be easily measured (Hobson, 1923; Whitehead, 1925; Hardy, 1940; Synge, 1951, 1970; Feynman, 1965; Schrödinger, 1996). For example, the area of a rectangle is difficult to measure. However, if one knows its length and width, and the relation that area is the product of length and width, the area can be calculated from the easily measurable quantities. Likewise, the circumference or area of a circle is relatively difficult to measure. However, if one measures the diameter and multiplies it by π, or the square of the diameter by $\pi/4$, one can easily obtain the circumference and area, respectively. In the same way, one can easily estimate the height of a tree from easily measurable quantities if one understands trigonometry and the definition of tangent.

My teaching was greatly influenced by a story that Hans Bethe told at a meeting at Cornell University commemorating the 50th anniversary of the chain reaction produced by Enrico Fermi. Bethe spoke about the difference between his graduate adviser, Arnold Sommerfeld, and his postdoctoral adviser, Enrico Fermi. He said that, in the field of atomic physics, Sommerfeld was a genius at creating a mathematical theory to describe the available data. Sommerfeld's skill, however, depended on the presence of data. Fermi, on the other hand, could come up with theories even if the relevant data were not apparent. He would make estimates of the data from first principles. For example, he estimated the force of the first atomic bomb by measuring the distance small pieces of paper flew as they fell to the ground during the blast in Alamogordo. Knowing that the force of the blast diminished with the square of the distance from the bomb, Fermi estimated the force of the bomb relative to the force of gravity. Within seconds of the blast, he calculated the force of the bomb to be approximately 20 kilotons, similar to which the expensive machines recorded (Fermi, 1954; Lamont, 1965).

In order to train his students to estimate things that they did not know, Fermi would ask them, "How many piano tuners are there in Los Angeles?" After they looked befuddled, he would say, "You can estimate the number of piano tuners from first principles! For example, how many people are there in Los Angeles? One million? What percentage has pianos? Five percent? Then there are 50,000 pianos in Los Angeles. How often does a piano need to be tuned? About once a year? Then 50,000 pianos need to be tuned in a year. How many pianos can a piano tuner tune in a day? Three? Then one tuner must spend 16,667 days a year tuning pianos. But since there are not that many days in a year, and he or she probably only works 250 days a year, then there must be around 67 piano tuners in Los Angeles."

My students apply the power of numbers to the study of cellular processes, including membrane transport, photosynthesis, and respiration, in order to get a feel for these processes and the interconversions that occur during these processes between different forms of energy. My students apply the power of numbers to the study of cell growth, chromosome motion, and membrane trafficking in order to be able to postulate and evaluate the potential mechanisms involved in these processes, and the relationships between these processes and the bioenergetic events that power them. Becoming facile with numbers allows the students to understand, develop, and critique theories. "As the Greek origin of the word [theory] implies, the Theory is the true *seeing* of things—the insight that should come with healthy sight" (Adams and Whicher, 1949).

Using the power of numbers to relate seemingly unrelated processes, my students are able to try to analyze all their conclusions in terms of first principles. They also learn to make predictions based on first principles. The students must be explicit in terms of what they are considering to be facts, what they are considering to be the relationship between facts, and where they are making assumptions. This provides a good entrée into research, because the facts must be refined and the assumptions must be tested (East, 1923).

I do not try to introduce any more terminology in my class than is necessary, and I try to explain the origin of each term. Some specialized terms are essential for precise communication in science just as it is in describing love and beauty. However, some terms are created to hide our ignorance, and consequently prevent further inquiry, because something with an official-sounding name seems well understood (Locke, 1824; Hayakawa, 1941; Rapoport, 1975). In Goethe's (1808) "Faust Part One," Mephistopheles says: "For at the point where concepts fail. At the right time a word is thrust in there. With words we fitly can our foes assail." Francis Bacon (1620) referred to this problem as the "Idols of the Marketplace." Often we think we are great thinkers when we answer a question with a Greek or Latin word. For example, if I am asked, "Why are leaves green?" I quickly retort, "Because they have chlorophyll." The questioner is satisfied, and says "Oh." The conversation ends. However, chlorophyll is just the Greek word for green leaf. Thus, I really answered the question with a tautology. I really said "Leaves are green because leaves are green" and did not answer the question at all. It was as if I was reciting a sentence from scripture, which I had committed to memory without giving it much thought. However, I gave the answer in Greek, and with authority ... so it was a scientific answer.

In "An Essay Concerning Human Understanding," John Locke (1824) admonished that words are often used in a nonintellectual manner. He wrote,

> *... he would not be much better than the Indian before-mentioned, who, saying that the world was supported by a great elephant, was asked what the elephant rested on; to which his answer was, a great tortoise. But being again pressed to know what gave support to the broad-backed tortoise, replied, something he knew not what. And thus here, as in all other cases where we use words without having clear and distinct ideas, we talk like children; who being questioned what such a thing is, which they know not, readily give the satisfactory answer, that it is something; which in truth signifies no more, when so used either by children or men, but that they know not what; and that the thing that they pretend to know and talk of is what they have no distinct idea of at all, and so are perfectly ignorant of it, and in the dark.*

Sometimes terms are created to become the shibboleths of a field, and sometimes they are created for political reasons, financial reasons, or to transfer credit from someone who discovers something to someone who renames it (Agre et al., 1995). Joseph Fruton (1992) recounted (and translated) a story of a conversation with a famous chemist in Honoré de Balzac's La Peau de Chagrin:

> *"Well, my old friend," said Planchette upon seeing Japhet seated in an armchair and examining a precipitate, "How goes it in chemistry?"*
>
> *"It is asleep. Nothing new. The Académie has in the meantime recognized the existence of salicine. But salicine, asparagine, vauqueline, digitaline are not new discoveries."*

"If one is unable to produce new things," said Raphael, "it seems that you are reduced to inventing new names."
"That is indeed true, young man."

I teach plant cell biology with a historical approach and teach "not only of the fruits but also of the trees which have borne them, and of those who planted these trees" (Lenard, 1906). This approach also allows them to understand the origins and meanings of terms; to capture the excitement of the moment of discovery; to elucidate how we, as a scientific community, know what we know; and it emphasizes the unity and continuity of human thought (Haldane, 1985). I want my students to become familiar with the great innovators in science and to learn their way of doing science (Wayne and Staves, 1998, 2008). I want my students to learn how the scientists we learn about choose and pose questions, and how they go about solving them. I do not want my students to know just the results and regurgitate those results on a test (Szent-Györgyi, 1964; Farber, 1969). I do not want my students to become scientists who merely repeat on another organism the work of others. I want my students to become like the citizens of Athens, who according to Pericles "do not imitate—but are a model to others." Whether or not my students become professional cell biologists, I hope they forever remain amateurs and dilettantes in terms of cell biology. That is, I hope that I have helped them become "one who loves cell biology" and "one who delights in cell biology" (Chargaff, 1986)—not someone who cannot recognize the difference between a pile of bricks and an edifice (Forscher, 1963), not someone who sells "buyology" (Wayne and Staves, 2008), and not someone who sells his or her academic freedom (Rabounski, 2006; Apostol, 2007).

Often people think that a science course should teach what is new, but I answer this with an amusing anecdote told by Erwin Chargaff (1986): "Kaiser Wilhelm I of Germany, Bismark's old emperor, visited the Bonn Observatory and asked the director: 'Well, dear Argelander, what's new in the starry sky?' The director answered promptly: 'Does your Majesty already know the old?' The emperor reportedly shook with laughter every time he retold the story."

According to R. John Ellis (1996),

> *It is useful to consider the origins of a new subject for two reasons. First, it can be instructive; the history of science provides sobering take-home messages about the importance of not ignoring observations that do not fit the prevailing conceptual paradigm, and about the value of thinking laterally, in case apparently unrelated phenomena conceal common principles. Second, once a new idea has become accepted there is often a tendency to believe that it was obvious all along—hindsight is a wonderful thing, but the problem is that it is never around when you need it!*

The historical approach is necessary, in the words of George Palade (1963), "to indicate that recent findings and present concepts are only the last approximation in a long series of similar attempts which, of course, is not ended."

I teach my students that it is important to be skeptical when considering old as well as new ideas. According to Thomas Gold (1989),

> *New ideas in science are not always right just because they are new. Nor are the old ideas always wrong just because they are old. A critical attitude is clearly required of every scientist. But what is required is to be equally critical to the old ideas as to the new. Whenever the established ideas are accepted uncritically, but conflicting new evidence is brushed aside and not reported because it does not fit, then that particular science is in deep trouble—and it has happened quite often in the historical past.*

To emphasize the problem of scientists unquestioningly accepting the conventional wisdom, Conrad H. Waddington (1977) proposed the acronym COWDUNG to signify the Conventional Wisdom of the Dominant Group.

In teaching in a historical manner, I recognize the importance of Thomas H. Huxley's (1853) warnings that "Truth often has more than one Avatar, and whatever the forgetfulness of men, history should be just, and not allow those who had the misfortune to be before their time to pass for that reason into oblivion" and "The world, always too happy to join in toadying the rich, and taking away the 'one ewe lamb' from the poor." Indeed, it is often difficult to determine who makes a discovery (Djerassi and Hoffmann, 2001). I try to the best of my ability to give a fair and accurate account of the historical aspects of cell biology.

My course includes a laboratory section and my students perform experiments to acquire personal experience in understanding the living cell and how it works (Hume, 1748; Wilson, 1952; Ramón y Cajal, 1999). Justus von Liebig (1840) described the importance of the experimental approach this way:

> *Nature speaks to us in a peculiar language, in the language of phenomena; she answers at all times the questions which are put to her; and such questions are experiments. An experiment is the expression of a thought: we are near the truth when the phenomenon, elicited by the experiment, corresponds to the thought; while the opposite result shows that the question was falsely stated, and that the conception was erroneous.*

My students cannot wait to get into the laboratory. In fact, they often come in on nights and weekends to use the microscopes to take photomicrographs. At the end of the semester, the students come over to my house for dinner (I worked my way through college as a cook) and bring their best photomicrographs. After dinner, they vote on the twelve best, and those are incorporated into a class calendar. The calendars are beautiful and the students often make extra to give as gifts.

In 1952, Edgar Bright Wilson Jr. wrote in *An Introduction to Scientific Research*, "There is no excuse for doing a given job in an expensive way when it can be carried through equally effectively with less expenditure." Today, with an emphasis on research that can garner significant money for a college or university through indirect costs, there is an emphasis on the first use of expensive techniques to answer cell biological questions and often questions that have already been answered. However, the very expense of the techniques often prevents one from performing the preliminary experiments necessary to learn how to do the experiment so that meaningful and valuable data and not just lists are generated. Unfortunately, the lists generated with expensive techniques often require statisticians and computer programmers, who are far removed from experiencing the living cells through observation and measurement, to tell the scientist which entries on the list are meaningful. Thus, there is a potential for the distinction between meaningful science and meaningless science to become a blur. I use John Synge's (1951) essay on vicious circles to help my students realize that there is a need to distinguish for themselves what is fundamental and what is derived.

By contrast, this book emphasizes the importance of the scientists who have made the great discoveries in cell biology using relatively low-tech quantitative and observational methods. But—and this is a big *but*—these scientists also treated their brains, eyes, and hands as highly developed scientific instruments. I want my students to have the ability to get to know these great scientists. I ask them to name who they think are the 10 best scientists who ever lived. Then I ask if they have ever read any of their original work. In the majority of the cases, they have never read a single work by the people who they consider to be the best scientists. This is a shame. They read the work of others ... but not the best. Interestingly, they usually are well read when it comes to reading the best writers (e.g., Shakespeare, Faulkner, etc.).

Typically, the people on my students' lists of best scientists have written books for the layperson or an autobiography (Wayne and Staves, 1998). Even Isaac Newton wrote a book for the layperson! I give my class these references and encourage them to become familiar with their favorite scientists first hand. The goal of my lectures and this book is to facilitate my students' personal and continual journey in the study of life.

My goal in teaching plant cell biology is not only to help my students understand the mechanisms of the cell and its organelles in converting energy and material matter into a living organism that performs all the functions we ascribe to life. I also hope to deepen my students' ideas of the meaning, beauty, and value of life and the value in searching for meaning and understanding in all processes involved in living.

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