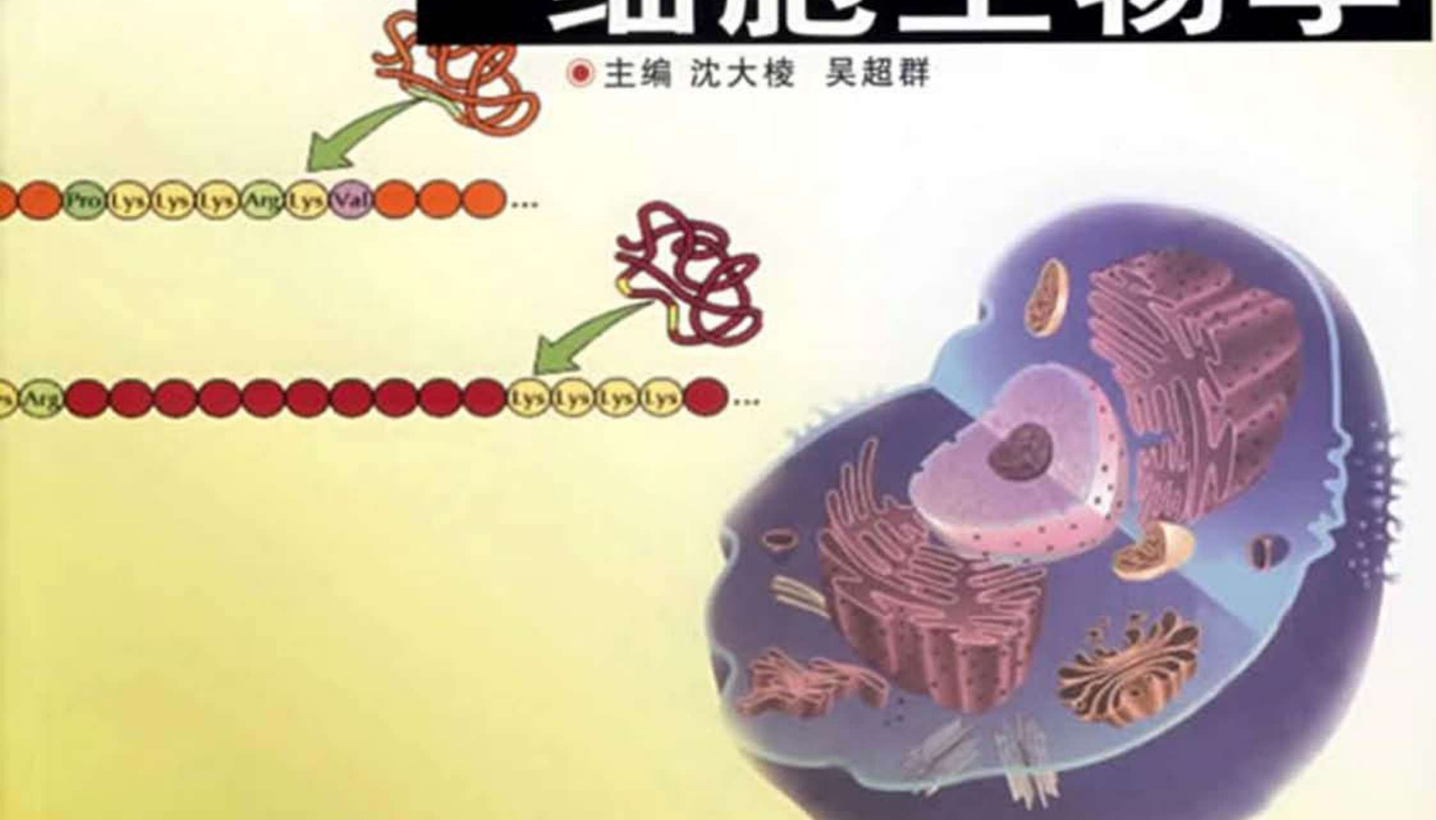
顾问 George R. Stark

双语教材

Cell Biology
细胞生物学

主编 沈大棱 吴超群



复旦大学出版社

• 双语教材 •

Cell Biology

细 胞 生 物 学

主编　沈大棱　吴超群

编者　(中文按姓氏笔画排序)
曲志才　山东曲阜师范大学
刘志学　上海大学
杨仲南　上海师范大学
李秀兰　山东曲阜师范大学
李　瑶　复旦大学
吴超群　复旦大学
沈大棱　复旦大学
张　森　上海师范大学
陈火英　上海交通大学
明　凤　复旦大学
June Liu Gentry Washington University in St. Louis, USA

顾问　George R. Stark, Lerner Research Institute, The Cleveland Clinic Foundation, Cleveland, Ohio, USA

復旦大學出版社

图书在版编目(CIP)数据

细胞生物学 = Cell Biology/沈大棱,吴超群主编.—上海:复旦大学出版社,2006.4

(双语教材)

ISBN 7-309-04903-9

Ⅰ.细… Ⅱ.①沈…②吴… Ⅲ.细胞生物学-双语教学-教材 Ⅳ.Q2

中国版本图书馆 CIP 数据核字(2006)第 011051 号

Cell Biology 细胞生物学

沈大棱 吴超群 主编

出版发行 复旦大学出版社 上海市国权路 579 号 邮编 200433

86-21-65642857(门市零售)

86-21-65118853(团体订购) 86-21-65109143(外埠邮购)

fupnet@fudanpress.com http://www.fudanpress.com

责任编辑 宫建平

总 编 辑 高若海

出 品 人 贺圣遂

印　　刷 上海申松立信印刷厂

开　　本 787 × 1092 1/16

印　　张 24.5

字　　数 703 千

版　　次 2006 年 4 月第一版第一次印刷

印　　数 1—3 100

书　　号 ISBN 7-309-04903-9/R·934

定　　价 45.00 元

如有印装质量问题,请向复旦大学出版社发行部调换。

内 容 简 介

本教材由复旦大学生命科学院细胞教学组牵头,组织国内外综合、师范、医学、农林等有关院校的11位多年从事细胞和分子生物学教学及科研的教授和专家,并在美国科学院院士、著名分子细胞生物学家 George R. Stark 教授直接指导下编写完成。在系统阐述细胞各部分的结构和功能的基础上,重点介绍了物质运输、信息传递、能量转换、周期调控、分化发育、癌变、免疫、衰老与凋亡等细胞的重大生命活动。正文全部用英语编写,语言上做到简练与通俗,科学上做到精确与先进;既介绍细胞生物学的基本概念和基本原理,又反映各领域的发展前沿。为便于读者自学并同时掌握中、英文双语概念,各章尾附有思考题,教材的附录为细胞生物学常用词汇的中文解释。

本双语教材可供综合大学、师范院校、医学院校、农林院校的本科生和研究生使用,也可供教师、科研人员与科教管理人员参考。

中 文 前 言

为了开展“细胞生物学”双语教学,我们曾先后尝试过直接选用国外原版教材、选编原版教材部分章节、自编英语讲义等方法,但总遇到一些问题。例如,国外原版教材篇幅太大,不适合国内教学要求与学时安排,且价格不菲,很难做到学生人手一册;选编原版教材部分章节有不够系统、不够全面的问题;自编英语讲义则由于印刷条件所限,图文不够清晰,同时内容上也受到教师个人专长范围的限制。所以,深感有必要联合各个高校长期从事“细胞生物学”教学和科研的教师,编写一部适合国内教学要求的双语教材。经过几年的筹划,我们组织编写了这本 *Cell Biology* 教材。

本教材由国内外 10 多位教授和专家参与编写,他们都是各院校系所多年从事“细胞生物学”教学和科研的学者,具备良好的英语基础和国外工作经历,拥有丰富的基础教学和双语教学经验。他们发挥各自所长,编写细胞生物学中自己比较熟悉并了解最新进展的内容。

为了适用生命科学包括理工、医农、师范本科“细胞生物学”基础课程的教学需要,本教材分为 14 部分,第 1 ~ 13 章全用英语编写;Glossary 是英汉对照细胞生物学术语,各词条用汉语解释,以方便初学者查阅。作为一门基础课教材,我们力求内容上的系统性、科学性和先进性,使之既能反映本学科的基本理论、基本概念和基本实验技术,又能反映学科最新的学术成果和发展方向。由于是用英语写作,还要求语言精确简练,为此我们在完成初稿后,特邀美国科学院院士、英国皇家科学院院士、美国克利夫兰医学中心莱纳研究所(Lerner Research Institute, The Cleveland Clinic Foundation, Cleveland, Ohio, USA)原所长、复旦大学荣誉教授、著名分子细胞生物学家 G. R. Stark 教授作为顾问对本教材各章进行严格仔细的审阅和修改,并为本教材作序。

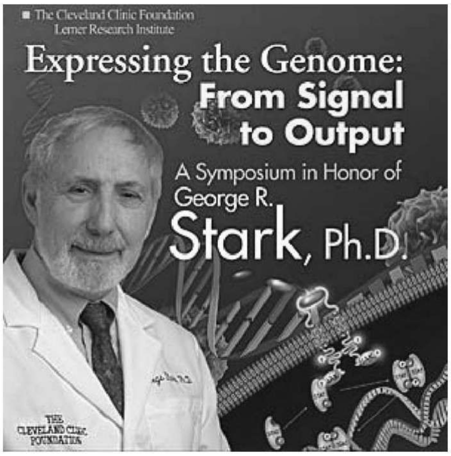
在本教材编写过程中,我们得到了复旦大学出版社的长期鼓励和支持,协助组织策划和落实了本教材的编写计划,提出了许多指导性意见,使本教材成为国内首批全英文教材之一。在编写过程中,博士生王敬文、陈东红等在整理稿件、文字打印、电脑扫描、图文校对等方面做了大量工作。在此我们一并深表感谢!

本教材由多位作者参与编写,虽经轮流传阅,相互修改,最后由主编统稿而成。由于水平和时间的限制,难免有疏漏和错误之处,敬请同行及读者批评指正,以便我们再版时纠正。

谨以本教材献给复旦大学“百年校庆”!

沈大棱　吴超群

2006 年 1 月



Preface

Dear Students:

You are about to embark upon a most exciting journey, and this textbook is your ticket for the first part. In recent years, spectacular advances have been made in our understanding of how cells work. Since cell biology is at the core of all life, it is one of the most active and exciting areas of current scientific research. I have been lucky to have been working in this field for more than 50 years, watching it grow and contributing my own small part. Therefore, I have a pretty good idea of what I am talking about! And, since I am an Honorary Professor at Fudan University, I have the opportunity to discuss a few things with you before you start on your own trips.

You will start learning about how cells work by studying this book. For many of you, this beginning will lead you to further journeys and many adventures. Hopefully, when you have completed this introductory course, you will begin to do research in some aspect of cell biology and begin to contribute to the large and growing pool of knowledge in this wonderful field. Who knows, some of you may even write a chapter or the preface for new cell biology textbook 50 years from now!

Since all organisms are made up of cells, we need to understand what cells are and how they function. We also need to understand how they develop and how they communicate with one another to maintain the essential functions of the organism. All of the information necessary is encoded in the DNA of each cell, and one of the major advances of recent years has been the determination of the complete sequences of the DNA of many species, including humans, worms, flies and some plants. The information encoded in the DNA is expressed in cells through the synthesis of messenger RNAs and proteins, and we now have powerful tools to allow us to determine simultaneously the amounts of the many thousands of messenger RNAs that are present in each cell, and our ability to analyze the patterns of protein expression is developing rapidly, especially though increased application of mass spectrometry to cell biology. While these tools have increased enormously what we can do, the hardest jobs still lie ahead. What does each protein do to help determine and support the functions of each of the many hundreds of different cell types that make up complex organisms such as us? Learning about how individual proteins function and about how they interact in complex networks inside cells will keep us all busy for many more years. But the payoff is fantastic! Apart from the beauty of knowledge of how living organisms function for its own sake, the more we know the more we can apply the information to understanding the causes of the many diseases that continue to plague us, leading eventually to better therapies and even to cures for many of them. The connection between cell biology and medicine is very tight, and the explosion in our current understanding of cell biology is already leading to major tools in the fights against cancer, heart disease, infectious disease and the other ailments from which humans suffer.

So take this first step on your journey seriously but with enjoyment and anticipation of all of the wonders that will follow. You have excellent guides in the professors who have prepared this excellent text. Good luck!

George R. Stark, Ph. D. , F. R. S.
Member of National Academy of Sciences, USA.
Fellow of the Royal Society, UK.

Honorary Professor, Fudan University;
Distinguished Scientist,
Cleveland Clinic Foundation;
Professor of Genetics,
Case Western Reserve University.

January 24, 2006,
Cleveland, USA

Contents

Chapter 1

Introduction to cell biology

1.1 What is cell biology

Cell biology is the application of molecular biological approaches to an understanding of life at the cellular level. Knowledge of the molecular basis of cell structure, cell function and cell interactions is fundamental to an understanding of whole organisms, since the properties of organisms are dependent upon the properties of their constituent cells.

1.1.1 Cell biology is the basis of modern biology

Cell biology is the modern biology, an academic discipline which studies the structure and physiological properties of cells, as well as their behaviors, interactions, and environment on a microscopic and molecular level. But two main features should be stressed in the modern cell biology.

Study the molecules within cells

Cell biology is a modern science, which is rooted in an understanding of the molecules within cells, and of the interactions between cells that allow construction of **multicellular organisms**. The more we learn about the structure, function, and development of different organisms, the more we recognize that all life processes exhibit remarkable similarities.

Cell biology concentrates on:

- Macromolecules and reactions, investigated by biochemists.
- The processes described by cell biologists.
- The gene control pathways identified by molecular biologists and geneticists.

Study the molecular similarities and differences between cell types

Understanding the composition of cells and how cells works is fundamental to all of the biological sciences. Appreciating the similarities and differences between cell types is particularly important to the fields of molecular cell biology. These fundamental similarities and differences provide a unifying theme, allowing the principles learned from studying one cell type to be extrapolated and generalized to other cell types. Research in cell biology is closely related to genetics, biochemistry, molecular biology and developmental biology.

1.1.2 Cell biology is in progress

All the concepts of cell biology continue to be derived from computational experiments and laboratory experiments. The powerful experimental tools that allow the study of living cells and organisms at higher and higher levels are being developed constantly. In this chapter, we address the current state of cell biology and look forward to what further exploration will uncover in the twenty-first century.

In this millennium, two gathering forces will reshape cell biology:

- The **genomics**, the complete DNA sequence of many organisms.
- The **proteomics**, the knowledge of all the possible shapes and functions that proteins employ.

1.2 The cell theory

The cell theory is the basis of molecular cell biology, and this theory is known as one of the three indispensable theories upon which the science of biology is built. These theories are: ①The theory of evolution; ②The cell theory; ③The theory of equilibrium thermodynamics.

The cell theory, or cell doctrine, states that all organisms are composed of similar units of organization, called cells. The concept was formally articulated in 1839 by Schleiden and Schwann, and has remained as the foundation of modern biology. The idea predates other great paradigms of biology including Darwin's theory of evolution (1859), Mendel's laws of inheritance (1865), and the establishment of comparative biochemistry (1940).

Ultrastructural research and modern molecular biology have added many tenets to the cell theory, but it remains as the preeminent theory of biology. The cell theory is to biology as atomic theory is to physics.

Just as an atom is the smallest particle of a chemical element, which can exist either alone or in combination and still possess the chemical and physical properties of that element, so then, a cell is the smallest entity, which can exhibit the characteristic of life.

1.2.1 Formulation of the cell theory

In 1663 Robert Hooke, an English scientist, discovered cells in a piece of cork, which he examined under his primitive microscope (Figure 1-1). Actually, Hooke only observed cell walls because cork cells are dead and without cytoplasmic contents. Hooke drew the cells he saw and also coined the word "cell". The word cell is derived from the latin word "cellula" which means small compartment. Hooke published his findings in his famous work, "*Micrographic: Physiological Descriptions of Minute Bodies Made by Magnifying Glasses* (1665)".

Ten years later, Anton van Leeuwenhoek (1632 ~ 1723), a Dutch businessman and a contemporary of Hooke used his own (single lens) monocular microscopes and was the first person to observe bacteria and protozoa. He looked at everything from rain water to tears. He saw moving objects that he termed "animacules." The tiny creatures appeared to be swimming.

Between 1680 and the early 1800's, it appeared that not much was accomplished in the study of cell structure. This may be due to the lack of quality lens for microscopes and the dedication to spend long hours of detailed observation over what microscopes existed at that time. Leeuwenhoek did not record his methodology for grinding quality lenses and thus microscopy suffered for over 100 years.

It is upon the works of Hooke, Leeuwenhoek, Oken, and Brown that Schleiden and Schwann built their cell theory. It was the German professor of botany at the university of Jena, Dr. Schleiden, who brought the nucleus to popular attention, and to assert its all-importance in the function of a cell.

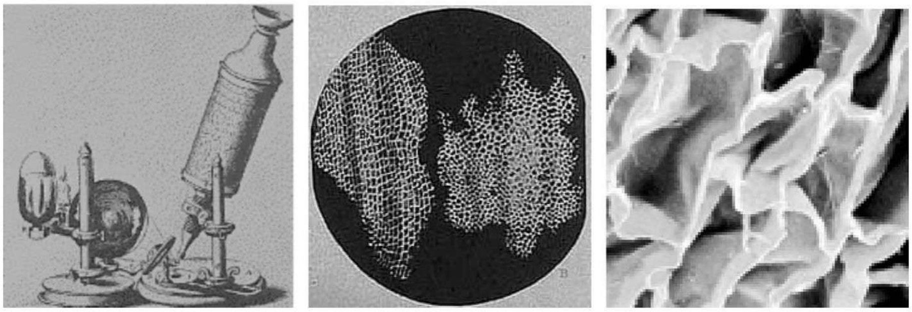


Figure 1-1 Hooke and his microscope. In 1663, Hooke examined under his primitive microscope(left). The small cell structures did not show up well or remained invisible(middle). The electron microscope not only showed more detail of previously known parts of the cell, but also revealed new parts. Cells and cell structures can now be examined at magnifications of up to 500 000 times and more(right).

The location of these nuclei at comparatively regular intervals suggested that they are found in definite compartments of the tissue, as Schleiden had shown to be the case with vegetables; indeed, the walls that separated such cell-like compartments one from another were in some cases visible. Soon Schwann was convinced that his original premise was right, and that all animal tissues are composed of cells not unlike the cells of vegetables. Adopting the same designation, Schwann propounded what soon became famous as the cell theory. So expeditious was his observations that he published a book early in 1839, only a few months after the appearance of Schleiden's paper. A most important era in cell biology dates from the publication of his book in 1839.

Schwann summarized his observations into three conclusions about cells:

- The cell is the unit of structure, physiology, and organization in living things.
- The cell retains a dual existence as a distinct entity and a building block in the construction of organisms.
- Cells form by free-cell formation, similar to the formation of crystals(**spontaneous generation**).

For a long time, people believed in spontaneous generation. They believed flies came from rotting meat and frogs from mud. It took a hundred years and many experiments to disprove those ideas and confirm that every cell comes from a pre-existing cell.

1.2.2 Modern tenets of cell theory

The cell doctrine reached its present-day eminence in 1896 with the publication of Wilson's *The Cell in Development and Heredity*, which was an accumulation of what was known about the roles of cells in embryology and chromosomal behavior.

For the first 150 years, the cell theory was primarily a structural idea. This structural view, which is found in most textbooks, describes the components of a cell and their fate in cell reproduction. Since the 1950's, however, cell biology has focused on DNA and its informational features. Today we look at the cell as a unit of self-control. The description of a cell must include ideas about how genetic information is converted to structure and function.

The modern tenets of the cell theory include:

- All known living things are made up of cells.
- The cell is the structural and functional unit of all living things.

- All cells come from pre-existing cells by division (not by spontaneous generation).
- Cells contain hereditary information which is passed from cell to cell during cell division.
- All cells are basically the same in chemical composition.
- All energy flow (**metabolism** & **biochemistry**) of life occurs within cells.

1.3 Cell is the basic unit of life

According to the cell theory, all living things are composed of one or more cells. Cells fall into **prokaryotic** and **eukaryotic** types. Prokaryotic cells are smaller (as a general rule) and lack much of the internal compartmentalization and complexity of eukaryotic cells. No matter which type of cell we are considering, all cells have certain features in common: cell membrane, DNA, cytoplasm, and ribosome.

1.3.1 The structure of cell

The cell is one of the most basic units of life. There are millions of different types of cells. There are cells that are organisms onto themselves, such as microscopic amoeba and bacteria cells. And there are cells that only function when part of a larger organism, such as the cells that make up your body.

The cell is the smallest unit of life in human bodies. In the body, there are brain cells, skin cells, liver cells, stomach cells, and the list goes on. All of these cells have unique functions and features. All have some recognizable similarities (Figure 1-2).

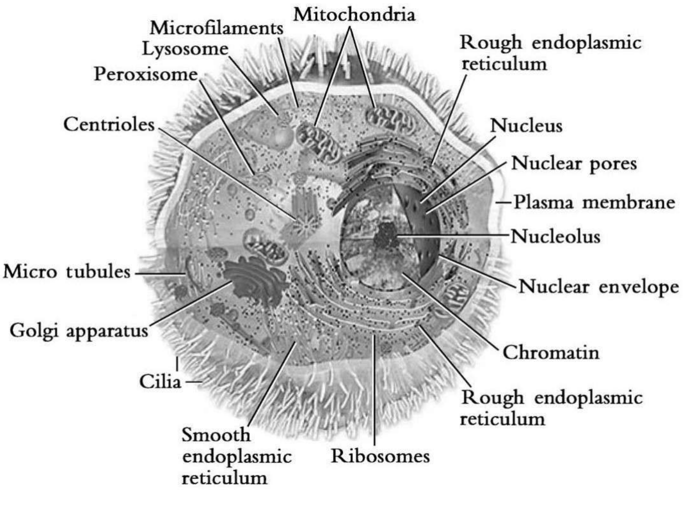


Figure 1-2 The structure of an animal cell

Plasma membrane

All cells have a "skin", called the **plasma membrane**, protecting them from the outside environment. The cell membrane regulates the movement of water, nutrients and wastes into and out of the cell. Inside of the cell membrane are the working parts of the cell.

Nucleus

At the center of the cell is the cell **nucleus**. The cell nucleus contains the cell's DNA, the genetic code that coordinates protein synthesis.

Organelles

There are many organelles inside of the cell — small structures that help carry out the normal operations of the cell. One important cellular organelle is the ribosome. **Ribosomes** participate in protein synthesis. The transcription phase of protein synthesis takes places in the cell nucleus. After this step is complete, the mRNA leaves the nucleus and travels to the cell's ribosomes, where translation occurs. Another important cellular organelle is the **mitochondrion**. Mitochondria (many mitochondrion) are often referred to as the power plants of the cell because many of the reactions that produce energy take place in mitochondria. Also important in the life of a cell are the **lysosomes**. Lysosomes are organelles that contain enzymes that aid in the digestion of nutrient molecules and other materials.

1.3.2 Differences between plant cell and animal cell

There are many different types of cells. One major difference in cells occurs between plant cells and animal cells. While both plant and animal cells contain the structures discussed above, plant cells have some additional specialized structures.

Plants do not have a skeleton for support and yet plants don't just flop over in a big spongy mess. This is because of a unique cellular structure called the **cell wall**. The cell wall is a rigid structure outside of the cell membrane composed mainly of the polysaccharide cellulose. The cell wall gives the plant cell a defined shape which helps support individual parts of plants.

Plant cells contain an organelle called the **chloroplast**. The chloroplast allows plants to harvest energy from sunlight. Specialized pigments in the chloroplast (including the common green pigment chlorophyll) absorb sunlight and use this energy to complete the chemical reactions.

1.3.3 Origin of the cell

In 1950, Stanley Miller designed an experimental test and recovered amino acids from C, H, O and N in abundance. Subsequent modifications of the atmosphere have produced representatives or precursors of all four **organic macromolecular** classes. The interactions of these molecules would have increased as their concentrations increased. Reactions would have led to the building of larger, more complex molecules. A pre-cellular life would have begun with the formation of nucleic acids. Chemicals made by these nucleic acids would have remained in proximity to the nucleic acids. Eventually the pre-cells would have been enclosed in a lipid-protein membrane, which would have resulted in the first cells.

But the question is how did the cell acquire a cell membrane? There are many theories that address this question but they fall into two categories, the thought requires that DNA or RNA be present; the other thought does not require DNA or RNA. There are no clear-cut answers to the nucleic acid question or the origin of a cell membrane, but there are a lot of theories. The most attractive theory is "RNA world theory". The RNA world theory describes that RNA is a close relative of DNA and it has been recently shown that RNA can act in an enzyme-like manner. In the RNA world scenario, RNA came first, playing the role of both DNA and enzyme proteins. This would make the first cell's chemistry very different from today's cells and would require its being superceded by today's cell's chemistry.

1.3.4 Three things make cell different from non-cell system

Life requires a structural compartment separate from the external environment in which macromolecules can perform unique functions in a relatively constant internal environment. These "living compartments" are cells. The cells differ from non-cell systems through three things:

- The capacity for replication from one generation to another. Most organisms today use DNA as the hereditary material, although recent evidence (ribozymes) suggests that **RNA** may have been the first nucleic acid system to have formed. Nobel laureate Walter Gilbert refers to this as the RNA world.
- The presence of enzymes and other complex molecules essential to the processes needed by living systems. Miller's experiment showed how these could possibly form.
- A membrane that separates the internal chemicals from the external chemical environment. This also delimits the cell from not-cell areas.

1.3.5 Microscope is needed to visualize cells

The small size of cells makes the use of microscopes necessary to view them (Figure 1-3). If two objects are too close together, they start to look like one object. With normal human vision the smallest objects that can be resolved (i. e., distinguished from one another) are about 200 μm (0.2 mm) in size.

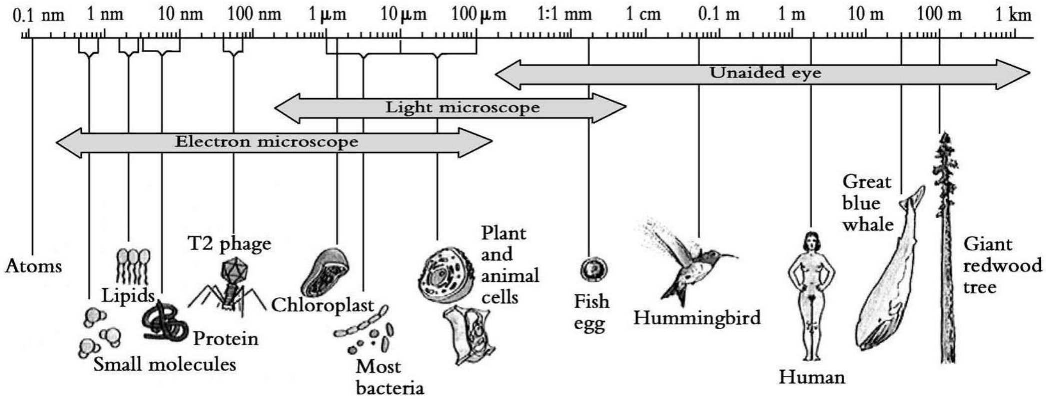


Figure 1-3 The relative sizes of biological objects ranging from atoms to tree (From Farabee, 2002)

Light microscopes use glass lenses and visible light and typically have a resolving power of 0.2 μm (0.2×10^{-6} m). Resolution depends on the wavelength of the illuminating light, but in general, resolution is about 1 000 times better than that of an unaided human eye. Living or killed and fixed cells may be viewed with light microscopes.

Electron microscopes have magnets, rather than glass lenses, to focus an electron beam. The wavelength of the electron beam is far shorter than that of light, and the resulting image resolution is far greater. This image is not visible without the use of either film or a fluorescent screen. Resolution is about 0.5 nm or 400 000 times finer than that of the human eye. Subcellular features can be seen only if the cells are killed and fixed with special fixatives and stains.

1.3.6 Techniques are developed to observe molecules inside cell

In addition the optical and electron microscope, now scientists are able to use a number of other techniques to probe the mysteries of the animal cell. Cells can be disassembled by chemical methods and their individual organelles and macromolecules isolated for study. The process of cell fractionation enables the scientist to prepare specific components, the mitochondria for example, in large quantities for investigations of their composition and functions. Using this approach, cell biologists have been able to assign various functions to specific locations within the cell. However, the era of fluorescent proteins has brought microscopy to the forefront of biology by enabling scientists to target living cells with highly localized probes for studies that don't interfere with the delicate balance of life processes.

1.3.7 Cells show two organizational patterns

Every cell has a plasma membrane, a continuous membrane that surrounds the fluids and other structures of a cell. The membrane is composed of a lipid bilayer with proteins floating within it and protruding from it. Living organisms can be classified into one of two major categories based on the location within the cell where the most genetic material is stored.

Prokaryotes have no nucleus or other membrane-bounded compartments. They lack distinct organelles, although some do have invaginated membrane structures.

Eukaryotes have a membrane-bounded nucleus and usually have other membrane-bounded compartments or organelles as well.

1.4 Diversity of cells

Cells fall into prokaryotic and eukaryotic types. Prokaryotic cells are smaller (as a general rule) and lack much of the internal compartmentalization and complexity of eukaryotic cells. No matter which type of cell we are considering, all cells have certain features in common: cell membrane, DNA, cytoplasm, and ribosomes. Both prokaryotic and eukaryotic cells include tremendous diversities in shape, structure, metabolism, and biological activity.

1.4.1 Diversity of prokaryotic cell

The cyanobacteria, formerly known as the blue-green algae, are the largest of the prokaryotes (organisms having prokaryotic cells). They contain chlorophyll and other pigments for photosynthesis. The pigments are not in membrane-bound chloroplasts, those organelles found in many plant cells. The pigments permeate throughout the entire cytoplasm.

Bacteria are the most abundant of all organisms

They are ubiquitous in soil, water, and as symbionts of other organisms. Many pathogens are **bacteria**. Most are minute, usually only 0.5-5.0 μm in size (though one type, *Thiomargarita namibiensis*, reaches 0.5 mm in diameter, and has a volume up to a million times that of the typical bacterium). They generally have cell walls, like plant and fungal cells, but with a very different composition (peptidoglycans). Many move around using flagella, which are different in structure from the flagella of other groups.