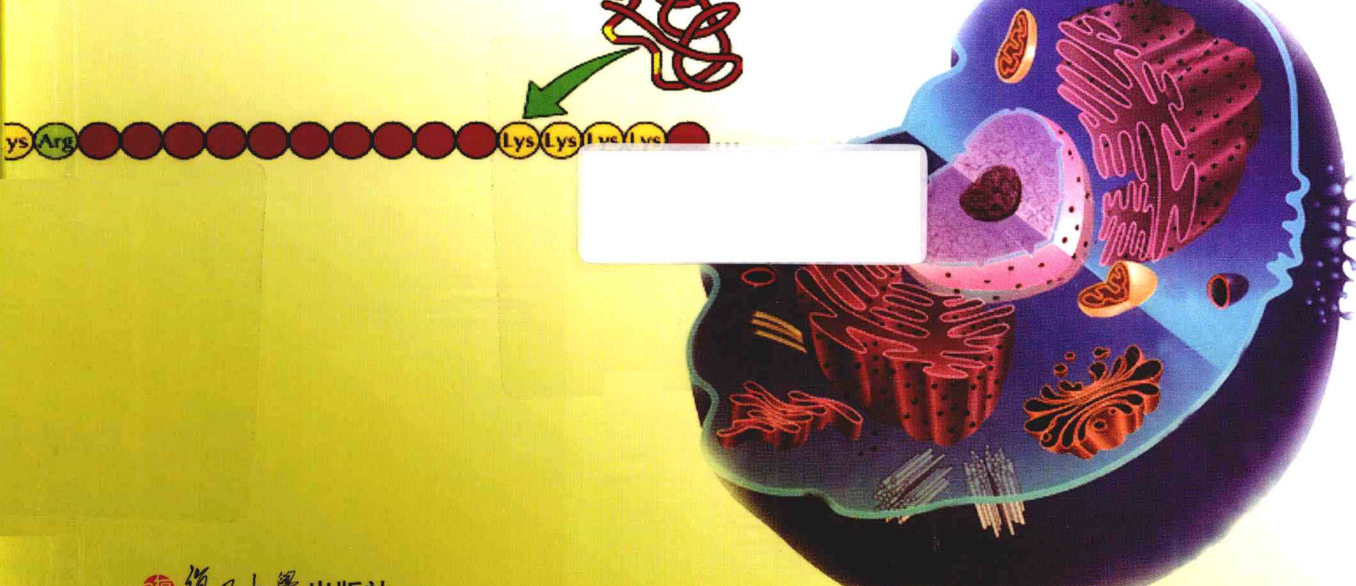
双语教材

Cell Biology

（第二版）

细胞生物学

主编 李 瑶 吴超群 沈大棱



復旦大學出版社

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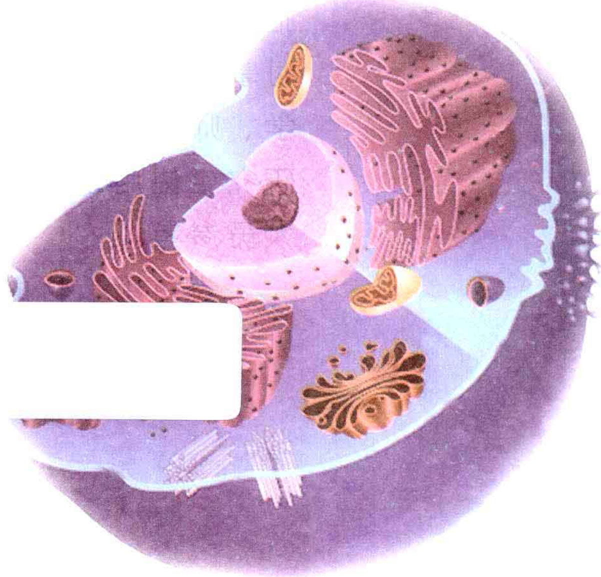

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内容简介

本教材是在第一版的基础上，由复旦大学生命学院细胞教学组牵头，组织国内多年从事细胞和分子生物学科研及教学的教授和专家改编完成。在系统阐述细胞各部分的结构和功能的基础上，重点介绍了细胞内外的物质运输、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。正文全文用英文撰写，语言上尽量做到简练与通俗，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。全书为彩色印刷，各章结尾附有思考题，附录为细胞生物学常用词汇的中文解释，便于读者自学同时掌握中英文的专业知识。本教材可供综合性大学、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。

为使用教材的教师免费提供PPT课件（详情见书尾附页）。

前　言

细胞生物学是一门迅猛发展的生命科学的重要基础学科，有关细胞的基础知识和相关研究是现代生命科学的基石。本教材的目的是使大学本科学生初步掌握本课程基本内容、基本原理、基本知识，为深入学习生命科学各科奠定基础。

为了让中国的大学生毕业后尽快完成从学习到研究的转变，为了我国开展细胞生物学双语教学，由本小组主持并邀请国内外综合、师范、农学、医学院校10多名教授专家和美国科学院院士一起研讨分工编写了双语教材，于2006年正式出版双语教材*Cell Biology*，并配合教材编写了中英文两套ppt课件。本双语教材受到采用学校师生的普遍欢迎，出版6年来，重印4次，发行量达到8,800册以上，并获2011年度上海市高校优秀教材二等奖。

由于细胞生物学发展迅速，知识面广，内容更新快，国外原版书每3～4年改版一次。另外，我们的第一版教材在使用过程中也发现了一些不足。为了与国际进展接轨，从去年开始，我们着手修订原教材。为了更好地完成任务，又邀请了几位刚从海外归国的年轻学者加入了改编工作，为本小组增添了活力。在内容上，基本保持了原书的框架，但做了部分调整，删除了和细胞生物学教学要求没有直接关系的原第二章，增加了细胞生物学应该有的重要内容“细胞质与核糖体”独立章节。因此，其他章节根据具体情况作了更新和调整，参考了最新的国外教科书和科学杂志、重要科学论文，适当介绍学科发展的前沿，在学习知识的同时也提高了同学们的专业英语水平，使学生增强专业论文的阅读能力；对专业词汇注明了中文解释，有助于学生的理解。考虑到不同院校的本科教学要求和学时数的限制，在内容上尽可能拓宽知识面，同时避免与其他学科如生化、分子生物学等学科的重复，强调基础知识，尽量控制其深度和难度。为了提高学习效果，本版改为彩图版。因此，本教材普遍适合于农、林、医、师范及综合性大专院校的本科双语教学和中文教学的参考书。

由于多方面的原因，参与第一版编写的部分编委未能加入第二版修订工作，但正是有了第一版的基础，才使得第二版的改编工作得以顺利完成，在此表示衷心的感谢！

由于本教材由多位作者共同参与编写，虽经轮流传阅，相互修改，最后由主编统稿而成。但由于水平有限，时间仓促，难免有疏漏和错误之处，欢迎热心的同行及读者批评指正，以便我们在今后的修订工作中不断改进。

编　者

2012年10月

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 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.

(1) 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 organism**s. 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: ① macromolecules and reactions, investigated by biochemists; ② the processes described by cell biologists; ③ the gene control pathways identified by molecular biologists and geneticists.

(2) 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 always developing

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: ①The **genomics**, the complete DNA sequence of many organisms; ②The **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: ① The theory of evolution; ② The cell theory; ③ The 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 what 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, an English scientist, Robert Hooke, 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, "Micrographia: Physiological Descriptions of Minute Bodies made by Magnifying Glasses (1665)."

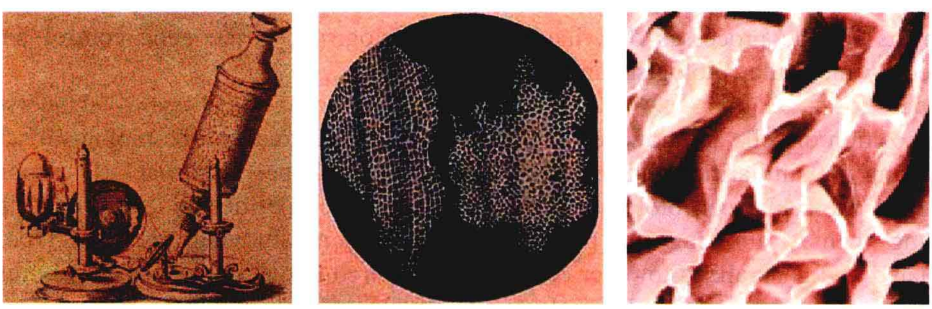

Figure 1-1 Hooke and his microscope. In 1663 Hooke examined under his primitive microscope (left). The small cell structures did not show up well or remained invisible (middle). The electron microscope not only showed more detail of previously known parts of the cell but also revealed new parts. Cells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

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 "animalcules." The tiny creatures appeared to be swimming.

Between 1680 and the early 1800's, it appears 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 asserted its all importance in the function of a cell.

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: ①The cell is the unit of structure, physiology, and organization in living things; ②The cell retains a dual existence as a distinct entity and a building block in the construction of organisms; ③Cells 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

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: ①All known living things are made up of cells; ②The cell is structural and functional unit of all living things; ③All cells come from pre-existing cells by division (not by spontaneous generation); ④Cells contain hereditary information which is passed from cell to cell during cell division; ⑤All cells are basically the same in chemical composition; ⑥All 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 than eukaryotic cells are. No matter which type of cells we are considering, all cells have certain features in common: cell membrane, DNA, cytoplasm, and ribosome.

1.3.1 The basic 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).

(1) Plasma membrane All cells have a "skin", called the **plasma membrane**, protecting it 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.

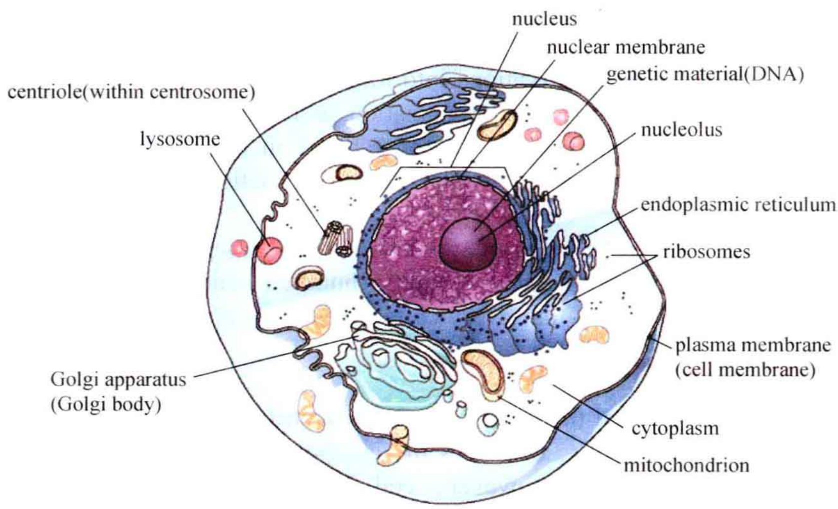

Figure 1-2 The structure of an animal cell (From: http://what-when-how.com)

(2) 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.

(3) 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 reaction.

1.3.3 Origin of the cell

In 1950, then-graduate student 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 (ribozyme) 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.

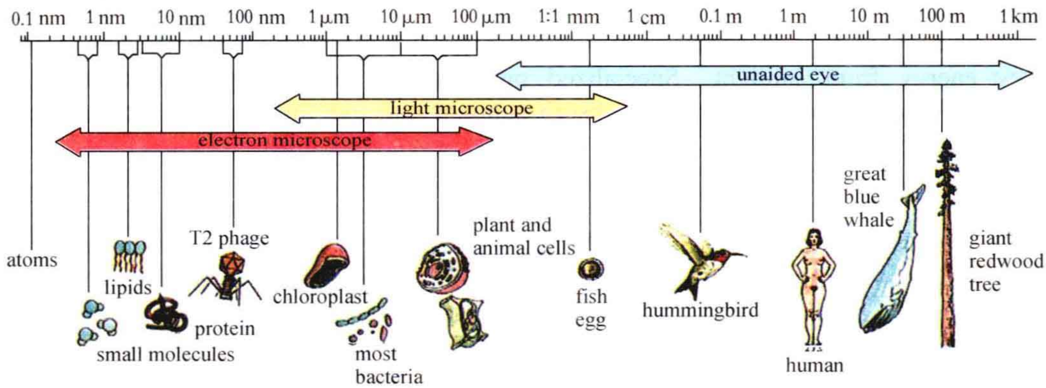

Figure 1-3 The relative sizes of biological objects ranging from atoms to tree (From: Farabee M J. 2002)

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, 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 From prokaryotes to eukaryotes

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 and eukaryotes (Figure 1-4).

Figure 1-4 Typical structures of prokaryotes and eukaryotes

Prokaryotes, such as archaea and bacteria are small, relatively simple cells surrounded by a membrane and a cell wall, with a circular strand of DNA containing their genes. They 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. The complex eukaryotic cell ushered in a whole new era for life on Earth, because these cells evolved into multicellular organisms.

Evidence supports the idea that eukaryotic cells are actually the descendents of separate prokaryotic cells that joined together in a symbiotic union.

1.4 The prokaryotic cell

Prokaryotes are cells without a distinct nucleus. They have genetic material but that material is not enclosed within a membrane. Prokaryotes include bacteria and cyanophytes. The genetic material is a single circular DNA strand and is located within the cytoplasm. Recombination happens through transfers of plasmids (short circles of DNA that pass from one bacterium to another). Prokaryoytes do not engulf solids, nor do they have centrioles or asters. Prokaryotes have a cell wall made up of peptidoglycan.

Common features of prokaryotic cells: ①All have a plasma membrane; ②All have a region called the nucleoid where the DNA is concentrated; ③The cytoplasm (the plasma membrane-enclosed region) consists of the nucleoid, ribosome (the molecular protein synthesis machines), and a liquid portion called the cytosol.

1.4.1 Specialized features of some prokaryotic cells

Most prokaryotic cells have a cell wall just outside the plasma membrane. The cell wall functions to prevent plasma membrane lysis (bursting) when cells are exposed to solutions with lower solute concentrations than the cell interior. It also protects the membrane.

In bacteria (but not in archaea), the cell wall is made of a polymer of amino sugars called peptidoglycan, which is covalently cross-linked to form one giant molecule around the entire cell. Some bacteria have another membrane outside the cell wall, a polysaccharide-rich phospholipid membrane. This membrane has embedded proteins that make it more permeable than the interior membrane. For some bacteria, this capsule provides a means to escape detection by the immune systems of the animals they infect. The capsule can prevent drying out of the cell and help the bacterium attack other cells. The capsule is not essential to cell life; if the cell loses the capsule, it can survive(Figure 1-5).

Some bacteria, including **cyanobacteria**, can carry on photosynthesis, that is, they have the ability to collect solar energy. Cyanobacteria have chlorophyll in the infolded plasma membrane for this purpose. Some bacteria have **mesosomes**, which are involved in cell division or in certain energy-releasing reactions. Like the photosynthetic membrane system, they are formed from plasma membrane infolding.

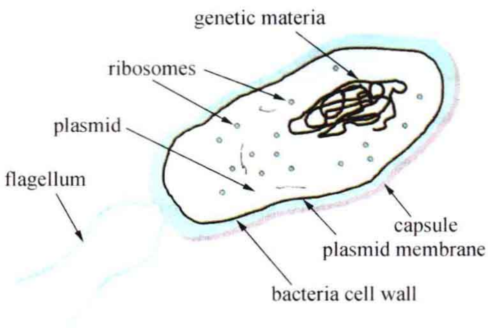

Figure 1-5 A typical bacterial cell. The bacterial cell is an example of a prokaryotic cell.

Some bacteria have **flagella**, locomotory structures shaped like a corkscrew. They spin like a propeller to move the bacteria. The flagella bear no structural similarity to the flagella found in eukaryotic cells, such as sperm cells. Some bacteria have piliform, threadlike structures that help bacteria adhere to one another during mating or to other cells for food and protection. Recent evidence suggests that some prokaryotes have an internal filamentous helical structure just below the plasma membrane. The proteins that make up this structure are similar to actin, a major component of the eukaryotic cytoskeleton.

1.4.2 Bacteria occupy major group of living organisms

Bacteria (singular, bacterium) are a major group of living organisms, most are microscopic and unicellular, with a relatively simple cell structure lacking a cell nucleus, cytoskeleton, and organelles such as mitochondria and chloroplasts. Their cell structure is further described in the article about prokaryotes, because bacteria are prokaryotes, in contrast to organisms with more complex cells, called eukaryotes. The term "bacteria" has variously applied to all prokaryotes or to a major group of them, depending on ideas about their relationships.

1.5 The eukaryotic cell

Animals, plants, fungi, and protists have a membrane-bounded nucleus in each of their cells and are classified as eukaryotes.

The autogenous and endosymbiotic hypotheses relate to possible ways in which eukaryote cells may have evolved from prokaryotic ancestors. The latter hypothesis is favored by most biologists. Briefly, this hypothesis suggests that the first eukaryotic cells resulted from symbiotic consortia between various types of prokaryotic cells. For example, the chloroplast resulted when a photosynthetic prokaryote entered another cell and survived. The mitochondrion is presumed to have evolved in a similar manner, but between non photosynthetic cells.

1.5.1 Eukaryotic cells share common features

Eukaryotic cells vary from animals, plants, to fungi and protists, but they have some common features which make them different from the prokaryotic cells.

(1) Common features The different types of eukaryotic cells show some similar features, they are: ①Eukaryotic cells tend to be larger than prokaryotic cells; ②Each of eukaryotic cells has a membrane-bounded nucleus; ③Eukaryotic cells have a variety of membrane-bounded compartments called **organelles**; ④Eukaryotes have a protein scaffolding called the cytoskeleton, which provides shape and structure to cells, among other functions.

(2) Compartmentalization is the key to eukaryotic cell function The subunits, or compartments, within eukaryotic cells are called organelles, which are responsible for specialized functions of the cell. The central organelle nucleus contains most of the cell's genetic material (DNA). The **mitochondrion** is a power plant and industrial park for the storage and conversion of energy. The endoplasmic reticulum and **Golgi apparatus** make up a compartment where proteins are packaged and sent to appropriate locations in the cell. The **lysosome** and vacuole are cellular digestive systems where large molecules are hydrolyzed into usable monomers. The **chloroplast** performs photosynthesis in plant cells. Membranes surrounding these organelles keep away inappropriate molecules that might disturb organelle function. They also act as traffic regulators for raw materials into and out of the organelle.

(3) Organelles can be studied by microscopy or chemical analysis Cell organelles were first detected by light and electron microscopy.

- The target specific macromolecules can be used to determine the chemical composition of organelles.
- The process of cell fractionation, another means by which cells can be examined.
- Microscopy and cell fractionation can be used as complements to each other, giving a complete picture of the structure and function of each organelle.

1.5.2 Plant cell structure

A plant has two organ systems: ①the shoot system; ②the root system. The shoot system is above ground and includes the organs such as leaves, buds, stems, flowers (if the plant has any), and fruits (if the plant has any). The root system includes those parts of the plant below ground, such as the roots, tubers, and rhizomes.

Plant cells are formed at **meristems**, and then develop into cell types which are grouped into tissues. Plants have only three tissue types: **dermal**, **ground**, and **vascular**. Dermal tissue covers the outer surface of herbaceous plants. Dermal tissue is composed of epidermal cells, closely packed cells that secrete a waxy cuticle that aids in the prevention of water loss. The ground tissue comprises the bulk of the primary plant body. Parenchyma, collenchyma, and sclerenchyma cells are common in the ground tissue. Vascular tissue transports food, water, hormones and minerals within the plant. Vascular tissue includes xylem, phloem, parenchyma, and cambium cells.

Like other eukaryotes, the plant cell is enclosed by a plasma membrane, which forms a selective barrier allowing nutrients to enter and waste products to leave. Unlike other eukaryotes, however, plant cells have retained a significant feature of their prokaryote ancestry, a rigid **cell wall** surrounding the plasma membrane. The cytoplasm contains specialized organelles, each of which is surrounded by a membrane. Plant cells differ from animal cells in that they lack centrioles and organelles for locomotion (cilia and flagella), but they do have additional specialized organelles. Chloroplasts convert light to chemical