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Textbook of Histology and Embryology

组织学与胚胎学

主 编 唐军民
李继承

原 著 Ovalle
Nahirney
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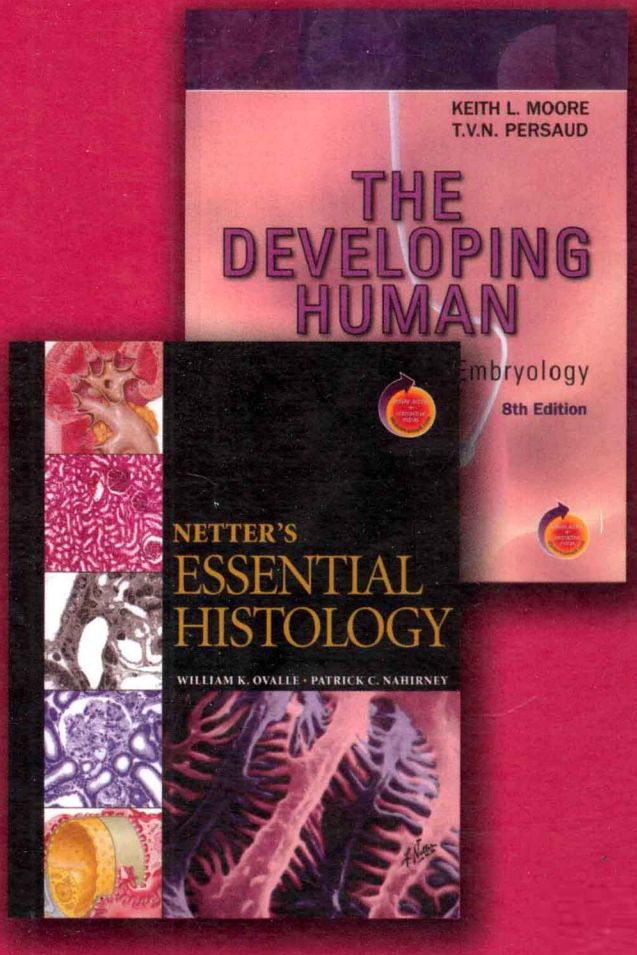
Persaud

《Netter 组织学》（第1版）和《胚胎学》（第8版）英文改编版



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北京大学医学出版社

图书在版编目（CIP）数据

组织学与胚胎学：英文 / 唐军民，李继承主编；—北京：北京大学医学出版社，2011.1
ISBN 978-7-5659-0045-7

Ⅰ. ①组… Ⅱ. ①唐…②李… Ⅲ. ①人体组织学—双语教学—医学院校—教材—英文
②人体胚胎学—双语教学—医学院校—教材—英文 Ⅳ. ①R32

中国版本图书馆CIP数据核字（2010）第208306号

北京市版权局著作权合同登记号：图字：01-2010-6082
Netter's Essential Histology
William K. Ovalle, Patrick C. Nahirney
ISBN-13: 978-1-929007-86-8
ISBN-10: 1-929007-86-8

The Developing Human,8th Edition
Keith L. Moore,T.V.N. Persaud
ISBN-13: 978-1-4160-3706-4
ISBN-10: 1-4160-3706-3

978-981-272-550-9
981-272-550-4

Elsevier (Singapore) Pte Ltd.
3 Killiney Road, #08-01 Winsland House I, Singapore 239519
Tel: (65) 6349-0200, Fax: (65) 6733-1817
First Published 2011
2011年初版

组织学与胚胎学

主　　编：唐军民　李继承
出版发行：北京大学医学出版社（电话：010-82802230）
地　　址：（100191）北京市海淀区学院路38号　北京大学医学部院内
网　　址：http://www.pumpress.com.cn
E-mail：booksale@bjmu.edu.cn
印　　刷：北京圣彩虹制版印刷技术有限责任公司
经　　销：新华书店
责任编辑：陈　奋　　**责任校对**：金彤文　　**责任印制**：张京生
开　　本：889mm×1194mm　1/16　　**印张**：33　　**字数**：1005千字
版　　次：2011年1月第1版　2011年1月第1次印刷
书　　号：ISBN 978-7-5659-0045-7
定　　价：108.00元

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改编版前言

随着我国科学技术的发展，高等医学教育也迎来了新一轮的发展。目前，许多学校在双语教学的基础上，也相继开展了留学生医学教学，并取得了许多经验。但在当前的组织学与胚胎学双语教学过程中，尚无全彩印刷的、权威的、公认的《组织学与胚胎学》英语教科书。虽然，各个医学院校或自编，或从几本国外教科书中部分节选，作为双语教学或留学生教学的教材，但由于自编的教材受到英语水平的限制，语言表达上往往不尽如人意。而从几本教材节选的内容，知识的系统性也难以保证。上述原因导致我国目前组织学与胚胎学的双语教学不规范，并影响教学质量。

Netter's Essential Histology 和 *The Developing Human*是世界范围内人体组织学与人体发育学的权威教科书，也是我国组织学与胚胎学的重要外文参考书。由于这两本教材的部分内容与我国的教学体系不同，同时价格昂贵，故原版教材难以成为我国的组织学与胚胎学教科书。但是该教材立足于临床，理论联系实际，语言专业、规范，图文并茂，具有独特、精准的编写风格，已被广泛认可。

为了提高我国的双语教学水平、方便教师授课和学生学习，北京大学医学出版社本着吸取国外优秀教材之精华的初衷，以国内教学大纲和国内优秀教材为标准，组织了全国十六所双语教学开展较好或有外国留学生的学校的二十余名有国外留学经历、外语水平较高，并有双语教学经验的专家教授，对Elsevier公司出版的*Netter's Essential Histology（1/E）* 和 *The Developing Human (8/E)* 进行缩减、改编和整合。其目的是在不改变原教材风格和基本内容的前提下，通过对这两部教材的内容进行删减缩编、改编整合，将两本相互独立的教材融合为一本适合于国内教学的《组织学与胚胎学》双语教材，其内容的广度和深度、编排的层次和逻辑关系等都与我国的《组织学与胚胎学》规划教材相对应。改编后的教材保留了原教材大部分插图，精减了少数与内容不太相关的插图和文字，内容充实、语言规范、图像精美、价格适中。同时，在内容上兼顾了临床医学及其他相关专业的需求。因此，本教材适用于临床医学、口腔、公共卫生专业的五、七、八年制学生和留学生的双语教学，也可作为教师的重要参考书。

在本教材的编写过程中，山东易创电子有限公司为该教材的审稿、定稿提供了极大的帮助，出版社的陈奋编辑也付出了辛勤的劳动，在此一并表示感谢。

由于改编和缩编外语教材是我们的首次探索和尝试，属于开创性的工作，疏漏和错误在所难免，欢迎老师和同学们在使用中提出宝贵意见和建议，我们将在今后的再版中不断给予新的补充和修改。

唐军民　李继承

2010年10月于北京

Contents

Section 1

Histology

Chapter 1
The Cell

The human body is organized into four **basic tissues** (**epithelial, muscle, nervous,** and **connective**) that consist of cells and associated *extracellular matrix.* The **cell** is the fundamental structural and functional unit of all living organisms. The body contains about 60×10^{12} cells—some 200 different types whose size and shape vary widely—but all have a common structural plan. The *eukaryotic cell* is a mass of **protoplasm** surrounded by an external **plasma (limiting) membrane.** The two components of the protoplasm are the **nucleus,** which holds the *genome* consisting of *chromosomes,* and the **cytoplasm,** a complex aqueous gel made of water (about 70%), proteins, lipids, carbohydrates, and organic and inorganic molecules. **Organelles** (specialized structures with functional capability) and **inclusions** (relatively inert, transitory structures) are in the cytoplasm. Except for mature erythrocytes, without a nucleus, most cells have one nucleus that conforms to the cell's shape. A few cells, such as osteoclasts and skeletal muscle cells, may be multinucleated. A **nuclear envelope** invests the nucleus, whose substance, called **chromatin,** contains one or more **nucleoli.** Internal cell structure is modified to reflect function: muscle cells, for example, are modified for contraction; nerve cells (or neurons), for conduction; connective tissue cells such as fibroblasts, for support; and glandular epithelial cells, for secretion (Fig.1-1).

1.1 ULTRASTRUCTURE AND FUNCTION OF CELL MEMBRANES

Membranes—semipermeable barriers that selectively regulate movement of ions, water, and macromolecules—are ubiquitous in cells. They vary in composition depending on cell type and location, but all consist of about 35% lipids, 60% proteins, and 5% carbohydrates. The **cell** (or **plasma**) **membrane** forms an external boundary. Intracellular membranes surround nuclei and membrane-bound organelles. Membranes are beyond the limit of resolution of a light microscope and are thus difficult to visualize without special techniques. By high-magnification electron microscopy, membranes have a trilaminar appearance: two dark lines separated by a thin electron-lucent zone. The entire **trilaminar membrane,** or **unit membrane,** is 5-8 nm thick. Membranes are made of a lipid bilayer, with a structure consistent with a highly dynamic **fluid mosaic model:** two hydrophilic phospholipid leaflets with polar phosphate heads that point outward. The hydrophobic fatty acid tail regions form the internal membrane framework. Cholesterol molecules, dispersed throughout the membrane, impart fluidity to it. **Intrinsic (integral) globular proteins** lie in the lipid bilayer and span the membrane thickness. **Extrinsic (peripheral) proteins** are also anchored to the membrane and associate with outside or inside surfaces of the bilayer. Carbohydrates often form a fuzzy coat called the *glycocalyx* on the outside of membranes. Membranes contain **channels** and *ion pumps* made of proteins that regulate the cell's internal milieu by creating electrical charge differences. Membranes also contain **receptors** for hormones and growth factors, such as receptors for neurotransmitters in plasma membranes of neurons and muscle cells (Fig.1-2).

1.2 ULTRASTRUCTURE AND FUNCTION OF THE NUCLEUS AND NUCLEOLUS

The nucleus—the largest, most conspicuous structure in the cell—contains genetic material. Size and shape may depend on cell type: usually spherical or ellipsoidal, a nucleus may also be elongated (as in columnar epithelial cells) or lobulated (as in polymorphonuclear leukocytes and megakaryocytes). Most cells have one nucleus; some (e.g., hepatocytes) may be *binucleated,* others (e.g., osteoclasts, skeletal muscle fibers), *multinucleated.* The nucleus consists of **nucleolus, chromatin, nuclear matrix,** and **nuclear envelope.** The nucleolus, the most conspicuous part of the nucleus, is a dense, ovoid, discrete area (up to 1 μm in

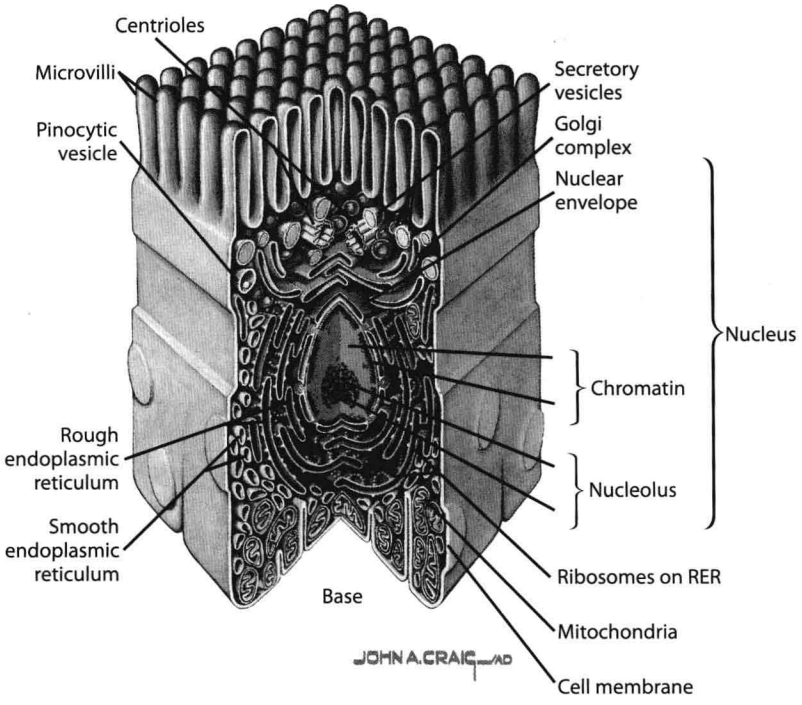
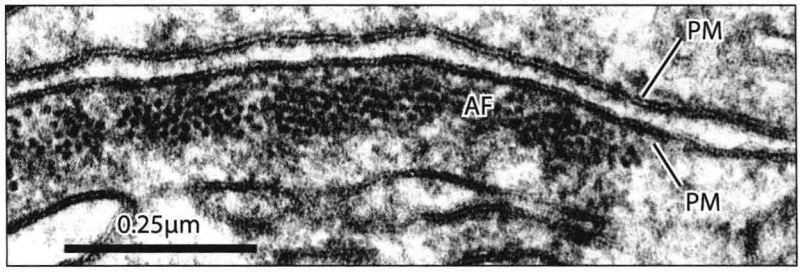


Figure 1-1 A composite cell cut open to show organization of its main components, as seen via electron microscopy. A plasma membrane surrounds the cell, which is polarized, with basal, lateral, and apical domains. Its cytoplasm contains various organelles and inclusions, which surround a nucleus. Some organelles are membrane bound, but some are not. The apical cell border has many finger-like projections called microvilli. Lateral cell borders are areas with intercellular junctions.



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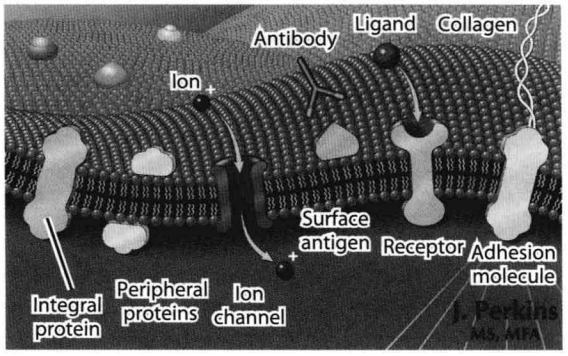


B

Figure 1-2 Cell Membrane. **A,** EM of cell membranes. Each plasma membrane (PM) of two adjacent cells has a trilaminar appearance. Actin filaments (AF) close to the cell surface are seen in transverse section. (*Courtesy of Dr. A. W. Vogl.*) **B,** Current rendition of the plasma membrane. The phospholipid bilayer is associated with integral and extrinsic proteins, which serve many functions—tissue organization via adhesion molecules, bidirectional transport of substances via ion channels, cell recognition by surface antigens, and intercellular communication via neurotransmitter and hormone receptors.

diameter) with no membrane around it. Its size, number, and location may depend on a cell's functional activity. The nucleolus is the site of *ribosomal RNA* (rRNA) transcription and production of *ribosomes.* It has a high content of RNA, so it is intensely basophilic by light microscopy. In EMs, the nucleolus shows two areas, the **pars granulosa** and **pars fibrosa,** that have no clear boundary between them. The pars granulosa, in peripheral nucleolar regions, is the main site of preribosome assembly. It consists of densely packed clusters of preribosomal particles (diameter: 15-20 nm) that are rich in ribonucleoprotein. The more central pars fibrosa contains a dense, irregular network of fine filaments (5 nm in diameter), rRNA genes, and transcription factors. The nucleolus disassembles in the prophase of mitosis but then reorganizes in daughter cells when cell division is complete (Figs.1-3*A* to *C*).

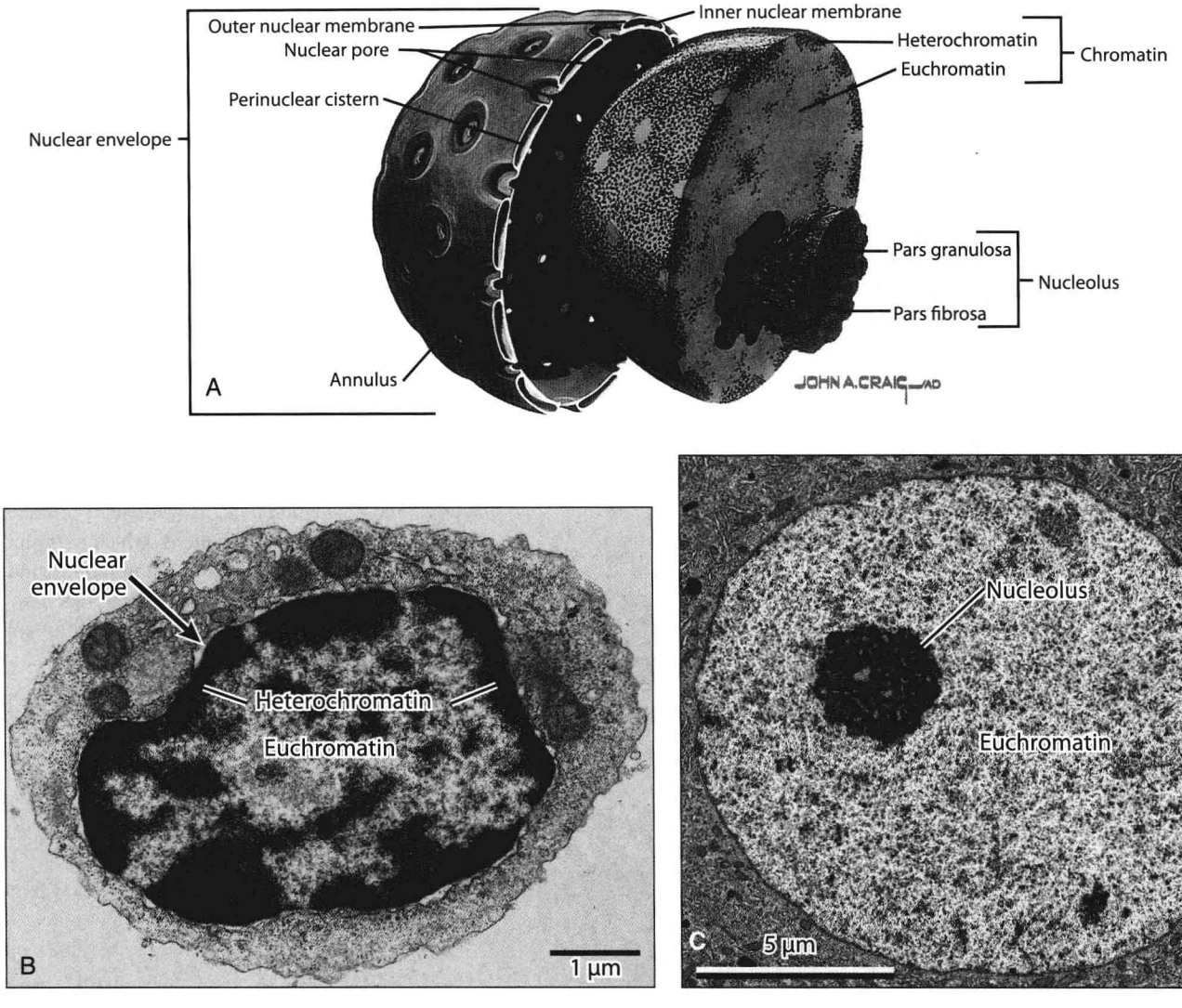


Figure 1-3 Nucleus and Nucleolus. **A,** Nuclear components. **B,** EM of a lymphocyte. Its nucleus shows euchromatin in the center and darker stained heterochromatin, which appears as dense patches, around the periphery. A discernible nuclear envelope separates nucleus from cytoplasm. **C,** EM of the perikaryon of a nerve cell in a spinal ganglion. This cell is active in protein synthesis, so its nucleus is mainly euchromatic with almost no heterochromatin. A spherical nucleolus, also in the plane of section, is eccentrically placed and electron dense; it lacks a membrane.

1.3 ULTRASTRUCTURE AND FUNCTION OF THE NUCLEUS: CHROMATIN AND MATRIX

Intensely stained substance of the nucleus is chromatin, which appears as irregular clumps. It consists chiefly of highly folded **DNA,** a nucleic acid, combined with structural proteins, mostly histones. It also contains nonhistone proteins and **RNA** that has been transcribed from DNA. Chromatin has a strong affinity for basic dyes, such as hematoxylin, used in light microscopy. Nuclear chromatin usually exists in two forms: **euchromatin** and **heterochromatin.** The pale or lightly stained euchromatin, which is dispersed regions of uncoiled **chromosomes,** is transcriptionally active and is prominent in protein-synthesizing cells. The condensed heterochromatin is transcriptionally inactive. It stains darker with basic dyes and in EMs looks more electron-dense compared with euchromatin. A typical nucleus has different amounts of the two forms. Heterochromatin is usually near the *nuclear envelope.* Intervening sponge-like areas between chromatin and nucleoli make up the **nuclear matrix.** It is rich in nonhistone proteins such as *condensins.* It also contains a meshwork of 10-nm intermediate filaments, called *nuclear lamins,* most of which adhere to the inner aspect of the nuclear envelope. The matrix, best seen via special techniques used with EMs, is a structural scaffold that organizes chromosomes during *meiosis* and *mitosis.* It also helps regulate gene transcription.

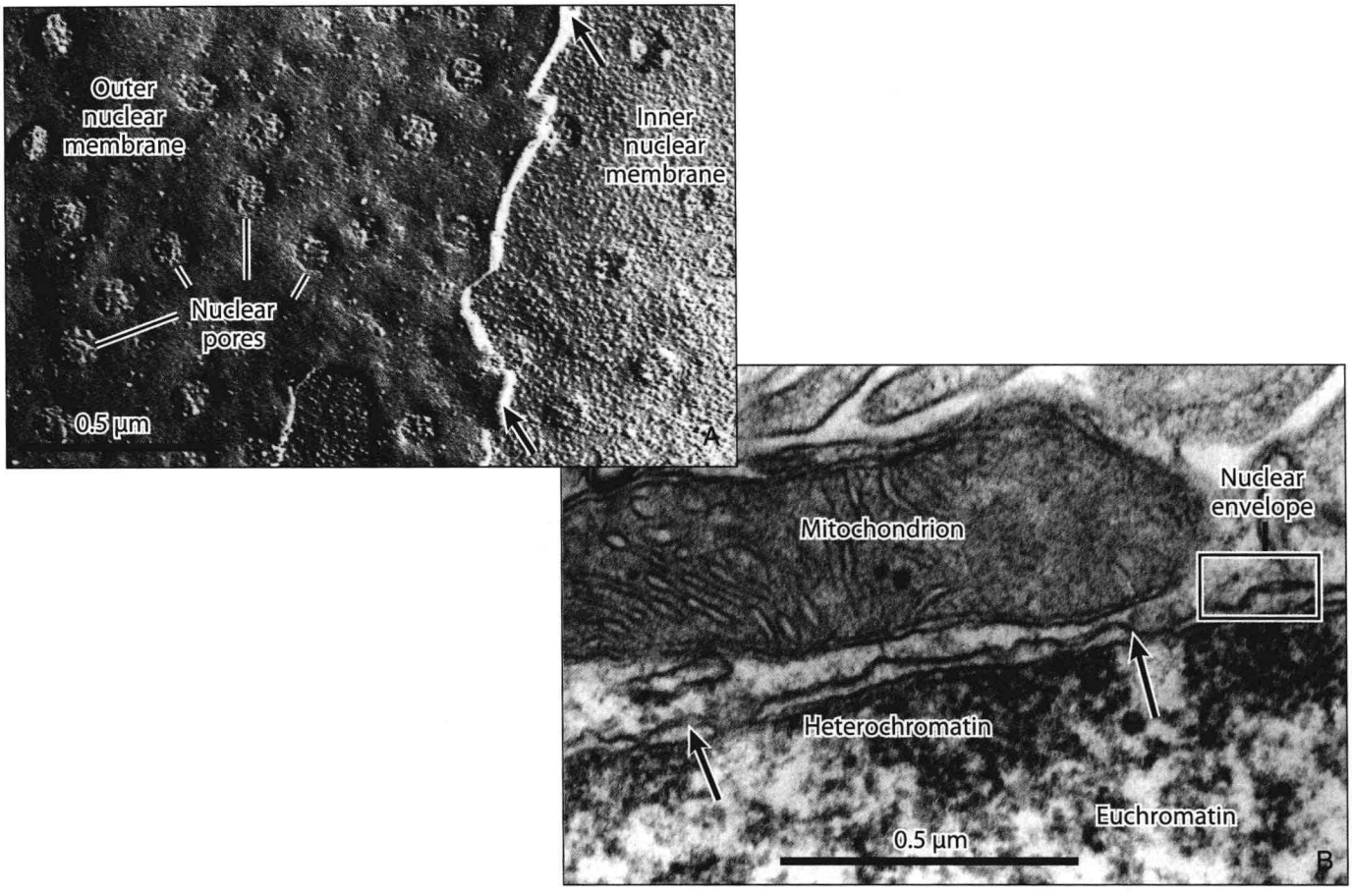


Figure 1-4 Nuclear Envelope. **A,** Freeze-fracture EM replica of the nuclear envelope. Outer and inner nuclear membranes are seen. The inner membrane has more intramembrane particles, which are integral membrane proteins, than the outer one. Part of the perinuclear space (*arrows*) is seen. Many nuclear pores perforate the envelope. Small spherical granules occupy the center of each pore complex. (*Courtesy of Dr. B. J. Crawford.*) **B,** EM of the nuclear envelope. A perinuclear space separates two concentric unit membranes (box). The smooth inner membrane directly contacts heterochromatin patches in the nucleus. The outer membrane is usually studded by ribosomes, but they are not seen here. Two nuclear pore complexes (*arrows*) cross the perinuclear space; fibrillar material seems to fill each pore aperture. A mitochondrion is in adjacent cytoplasm. (*Courtesy of Dr. W. A. Webber.*)

1.4 ULTRASTRUCTURE AND FUNCTION OF THE NUCLEAR ENVELOPE

A **nuclear envelope** encloses the nucleus of interphase cells and separates nucleus from cytoplasm. It consists of two parallel **unit membranes** separated by a narrow space (10-70 nm wide) termed the **perinuclear space (cisterna).** The **outer membrane** is studded externally by **ribosomes** and is continuous with cytoplasmic *rough endoplasmic reticulum* (RER). Thus, the perinuclear space is continuous with the RER lumen. The **inner membrane** lacks ribosomes, and its innermost surface is in contact with clumps of **heterochromatin** in the nucleus. Many small octagonal apertures, called **nuclear pores,** perforate the envelope. About 10 nm in diameter, they permit selective, bidirectional exchange of small molecules, ribosomal subunits, and other substances between nucleus and cytoplasm. Their number and distribution vary widely according to activity and type of cell; they are especially numerous in metabolically active cells. The outer rim of each pore forms by fusion of outer and inner nuclear membranes. A **nuclear pore complex** spanning the opening of each pore consists of eight proteins, or *nucleoporins,* around a central plug or granule. This complex is a molecular sieve and allows passive diffusion of molecules smaller than 10 nm but requires larger molecules to be transported by an energy-dependent mechanism that opens the pore. A meshwork of **intermediate filaments** associated with the nuclear side of the envelope consists of *lamins,* proteins that make up the *nuclear lamina.* These lamins maintain nuclear shape, help reinforce the nuclear envelope, and anchor ends of chromosomes (Figs.1-4*A* and *B*).

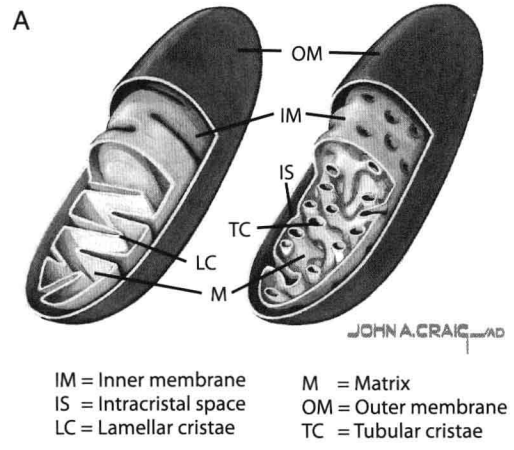
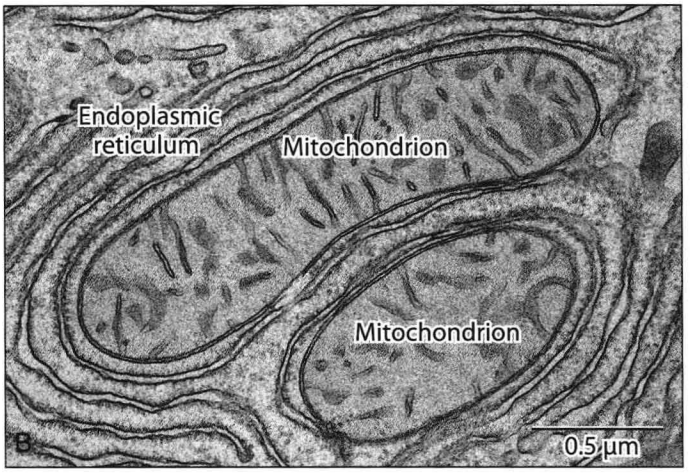
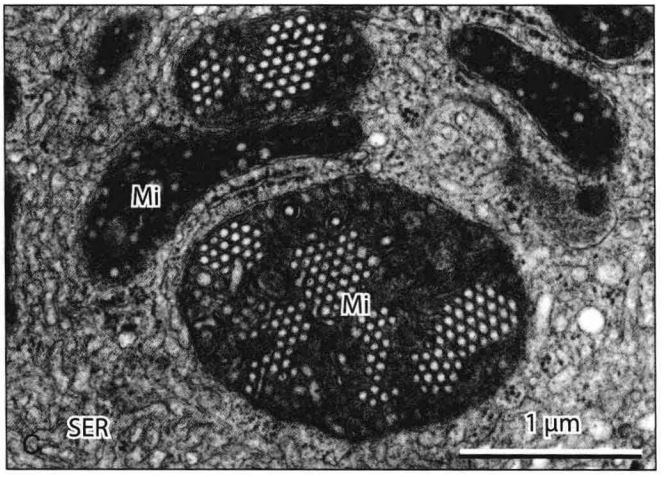


Figure 1-5 Mitochondria. **A,** Mitochondria with shelf-like and tubular cristae. **B,** EM of mitochondria in a hepatocyte. Their shape varies with plane of section and type of cell. Here, one is elongated; the other, more ovoid. Each has thin, shelf-like cristae that project into the mitochondrial matrix. Endoplasmic reticulum cisternae are in the cytoplasm. **C,** EMs of mitochondria in two different cells. The mitochondria in a steroid-secreting cell have tubular, not shelf-like, cristae and a dense mitochondrial matrix. Abundant smooth endoplasmic reticulum (SER) is in the cytoplasm. (*B Courtesy of Dr. D. M. Pfeiffer.*)





1.5 ULTRASTRUCTURE AND FUNCTION OF MITOCHONDRIA

Mitochondria are the most recognizable membrane-bound organelle. They are usually scattered throughout the cytoplasm of most cells, but they often concentrate in specific areas where high energy utilization, in the form of ATP, occurs. Such areas include apical regions of ciliated cells, basal areas of ion-transporting cells, and subsarcolemmal areas of skeletal and cardiac muscle cells. Their number and size vary with metabolic activity and type of cell: mature erythrocytes have none; a hepatocyte has up to 2500. They are 1-10 µm in size and may be elongated, spherical, or pleomorphic. These very dynamic organelles show constant motion, fusion, and division in cells. EMs reveal that two membranes separated by an intermembrane space of 8-10 nm invest them. The outer mitochondrial membrane has a smooth contour, which corresponds to the organelle's shape. The membrane consists mostly of a large channel-forming protein, porin, which increases membrane permeability for passage of molecules and metabolites for ATP synthesis. The inner mitochondrial membrane, however, shows transverse shelf-like or tubular folds—the cristae. They project into the inner chamber of the organelle, called the mitochondrial matrix, which has a finely granular increased electron density (Figs.1-5*A* to *C*).

Mitochondrial **cristae** vary greatly in size, shape, and number depending on cell type and metabolic activity. Cristae greatly increase surface area for ATP synthesis and reactions related to *electron transport, Krebs citric acid cycle,* and *oxidative phosphorylation.* The **matrix** contains many enzymes needed for oxidation reactions of the Krebs cycle. Cristae usually, but not always, extend across the interior of a mitochondrion. Most cells have flattened, lamellar cristae, which are usually perpendicular to the longitudinal axis of the mitochondrion. Tubular and tubulovesicular cristae are most common in **steroid-secreting cells,** where cristae also contain enzymes for *steroidogenesis.* Unlike other organelles, mitochondria have a degree of autonomy in a cell. They have their own closed-loop *DNA, RNA,* and *ribosomes* in the matrix.

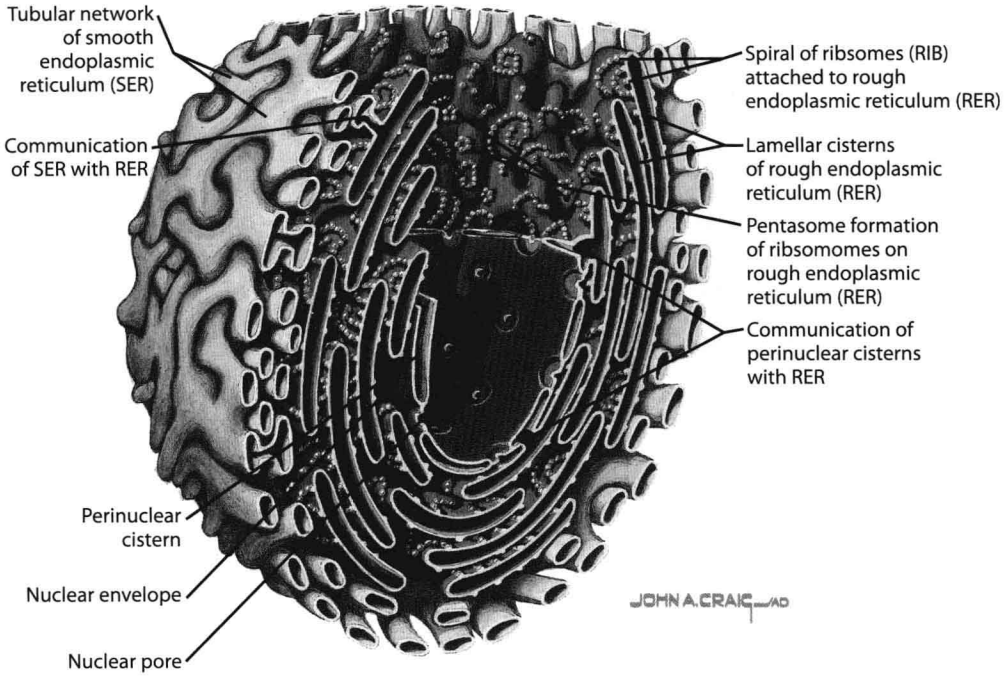


Figure 1-6 Three-dimensional schematic of the ER. This organelle is a continuous array of membrane-bound tubules, vesicles, and cisternae. A smooth-surfaced membrane encloses a central lumen, which is separated from the cytoplasm. Tubules often have flattened expansions called cisternae. Communications exist between RER and SER. The perinuclear space of the nuclear envelope is also continuous with the RER.

1.6 ULTRASTRUCTURE AND FUNCTION OF ENDOPLASMIC RETICULUM

The **endoplasmic reticulum** (ER) is a tortuous, communicating network of slender **tubules,** small circular **vesicles,** and flattened membranous **sacs (cisternae).** Its amount, distribution, and complexity vary widely depending on cell type and function. The anastomosing tubules may be scattered singly in the cytoplasm, but they often occur as stacks of multiple, parallel cisternae. The central cavity of the ER is separated from the cytoplasm by a closed membrane that is thinner but looks like the cell's plasma membrane. The two major forms of this delicate organelle are **smooth (SER)** and **rough (RER).**

Ultrastructure and Function of Smooth Endoplasmic Reticulum

The SER consists of smooth-surfaced membranes lacking ribosomes and thus appears agranular in EMs. The many functions of the SER depend on location. In hepatocytes, SER participates in carbohydrate metabolism. It uses enzymes (such as glucose-6-phosphatase) in its membranes to convert *glycogen* to *glucose.* Hepatocytes have abundant SER that routinely degrades lipid-soluble drugs (such as barbiturates) and alcohol, via various *drug-metabolizing enzymes* (such as cytochrome P450) on its surface. Steroid-secreting cells (such as those in ovary, testis, and adrenal gland) that store cholesterol have large amounts of SER, which functions in lipid and lipoprotein synthesis. In muscle cells, SER, called **sarcoplasmic reticulum,** engages in calcium ion regulation, which is critical for contraction to start (Fig.1-6).

Ultrastructure and Function of Rough Endoplasmic Reticulum

External **ribosomes** on the RER produce a rough or granular appearance in EMs, like small beads or coarse sandpaper—thus the term *rough.* RER consists of an interconnecting network of membrane-enclosed **cisternae** and **vesicles.** Its membranes are continuous with the outer membrane of the *nuclear envelope.* Ribosomes sit on the outer (cytoplasmic) surfaces of RER cisternae and form rosettes or a linear pattern. **Polyribosomes,** which are ribosomes connected by messenger **RNA** (mRNA) strands, also bind to external RER surfaces. RER engages in synthesis and export of *proteins* and *glycoproteins.* It is the site of translation, folding, and transport of newly formed proteins that become part of the cell membrane as *integral membrane proteins* and *transmembrane receptors* or that are proteins secreted by *exocytosis.* Ribosomes assemble **polypeptides** that are threaded into cisternae lumina. Newly formed protein is then folded into its native configuration. Once proteins are synthesized, most travel to the **Golgi complex** in *transfer vesicles.* The RER membrane has a receptor to bind the larger ribosome subunit and an adjacent pore to permit newly formed protein to enter and be sequestered in the RER lumen. Many different cell types that synthesize and secrete proteins contain an extensive, well-developed RER (Figs.1-7*A* and *B*).

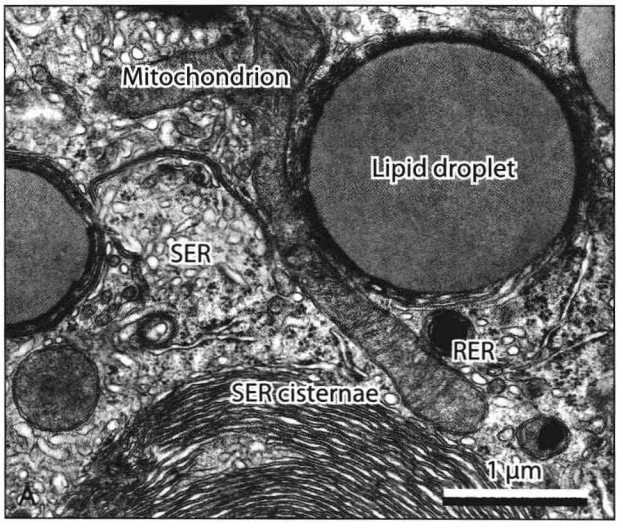


Figure 1-7A EM of part of a hepatocyte showing sagittal and cross-sectional SER. Abundant in hepatocytes, SER exists as small, branching tubules and multiple stacks of flattened cisternae. Here, the SER is closely associated with lipid droplets. A pleomorphic mitochondrion and a few profiles of RER also occupy the cytoplasm.

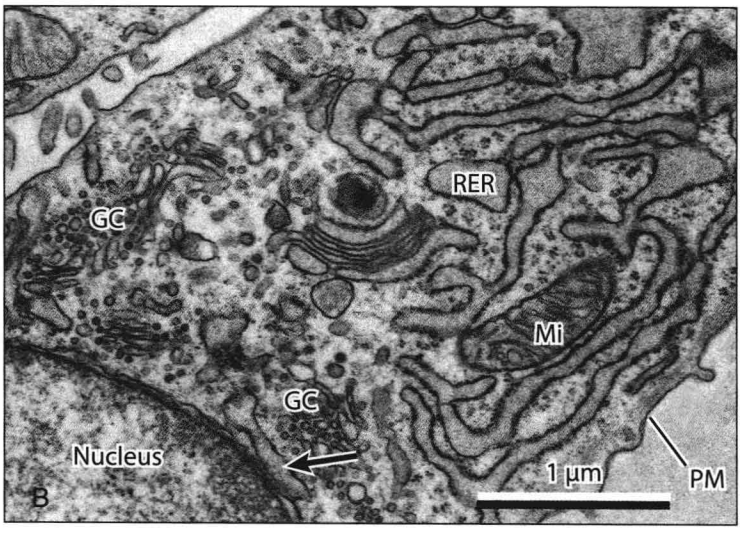


Figure 1-7B EM of part of a fibroblast in a growing tendon. The RER consists of an extensive network of branching membrane-bound tubules, studded externally with ribosomes. Its luminal contents are moderately electron dense and amorphous. Note the continuity of the RER and perinuclear space (*arrow*). Many free ribosomes are in the cytoplasm. In cells secreting protein for export, abundant RER is usually associated with one or more supranuclear Golgi complexes (GC). A mitochondrion (Mi) and plasma membrane (PM) are also seen.

1.7 ULTRASTRUCTURE AND FUNCTION OF RIBOSOMES

Ribosomes are small, spherical, electron-dense particles that synthesize proteins. Of uniform size, their diameter is 15-20 nm. They consist mostly of **RNA** and associated proteins. **Free ribosomes** in the cytoplasm occur as single particles or rosette-like clusters, termed **polyribosomes,** which consist of several ribosomes arranged along a thread of mRNA. Single ribosomes are inactive; polyribosomes actively synthesize protein by assembling amino acids into polypeptides. Ribosomes may also be attached to membranes of RER and to the **outer nuclear membrane.** Free ribosomes synthesize proteins for internal use by the cell, but ribosomes attached to RER synthesize proteins for export from cells or proteins destined for lysosomes. Ribosomes are small and thus below the limit of resolution of the light microscope, but their polyanionic nature makes them strongly basophilic because they have an affinity for basic dyes such as hematoxylin. In H&E-stained sections, they impart **cytoplasmic basophilia** to cells actively synthesizing protein. A high-resolution EM reveals that each ribosome consists of two unequal-size subunits that bind together during mRNA translation. The **large subunit** contains two RNA molecules and about 49 proteins; the **small subunit,** one RNA molecule and about 33 small proteins. Ribosomal subunits and their associated proteins are synthesized in the *nucleolus* and reach the cytoplasm via *nuclear pores.* Ribosomes, with binding sites for both mRNA and transfer RNA *(tRNA),* translate a coded genetic message from mRNA that is first transcribed in the nucleus. Translation involves movement of a ribosome along the mRNA chain, and the two subunits perform different functions in translation. tRNA transports amino acids to ribosomes for polymerization and polypeptide synthesis. mRNA decoding and polypeptide synthesis occur in a cavity between the subunits (Figs.1-8*A* and *B*).

1.8 ULTRASTRUCTURE AND FUNCTION OF THE GOLGI COMPLEX

The **Golgi complex** (or apparatus) was first discovered in neurons by the neurohistologist Camillo Golgi in 1898. He used the light microscope with silver stains, which he developed to study and describe the Golgi. He called it the *apparato reticolare interno,* and it now bears his name. The ultrastructural complexity of this dynamic organelle was not fully understood until the use of electron microscopy in the mid-1950s. Located in the center of the cell, the *cytocentrum,* the Golgi is close to the nucleus and centrosome. It is a complex array of flattened, slightly curved, closely packed **membrane-bound sacs (cisternae)** with associated **vesicles** and larger **vacuoles.** This highly polarized, compartmentalized organelle has convex and concave sides and three functionally distinct compartments: a **cis-Golgi network** of vesicles on the convex side, a

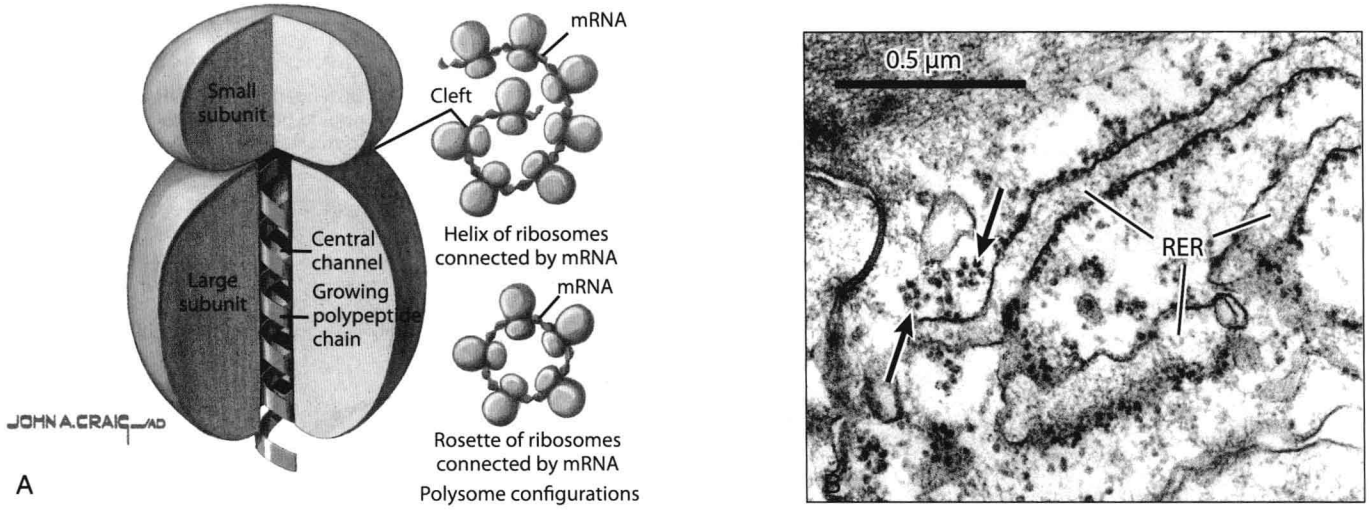


Figure 1-8 Ribosomes. **A,** Section of a single ribosome. **B,** Higher magnification EM of part of a protein- synthesizing cell. Several RER cisternae (RER) with attached ribosomes are seen. The cytoplasm also shows free ribosomes, many of which are rosettes (*arrows*) attached by thin strands of mRNA. (*Courtesy of Dr. B. J. Crawford.*)

medial compartment of stacks of flattened **saccules,** and on the concave side a **trans-Golgi network** of vesicles and vacuoles for distribution and sorting of secretory products. Some cells have one Golgi complex; others, which actively synthesize proteins and polysaccharides, have many. The Golgi complex adds proteins to sugars to form glycoproteins, assembles polysaccharides, elaborates membrane lipids, and produces **lysosomes** that are kept by cells.

A major role of the Golgi complex is to sort and package secretory proteins that are produced in the RER. By budding and fusing of **vesicles,** newly synthesized secretory material in the lumen passes from the proximal *(cis)* to the distal *(trans)* side of the organelle. **Transfer vesicles** from the RER fuse with the *cis*-Golgi complex to then deliver newly formed protein into flattened **saccules,** where protein is chemically modified. Each medial compartment saccule contains a different group of processing enzymes in its membranes—the *integral membrane proteins.* These chemical reactions, termed *posttranslational modifications,* include proteolytic processing of protein precursors, glycosylation, phosphorylation, hydroxylation, and sulfation. The endoplasmic reticulum and Golgi complex also produce most lipids, especially those associated with membranes, which are kept by cells and organelles. Cytoplasmic *microtubules* closely associated with the Golgi complex help move and transfer vesicles and **vacuoles** to different parts of a cell. Vesicles associated with the **trans-Golgi network** have one of three purposes. They may form **secretory vesicles** that release contents by exocytosis to the cell exterior; they may fuse with the *plasma membrane* for insertion of proteins and lipids into it; or they may become *lysosomes* (Figs.1-9*A* and *B*).

1.9 ULTRASTRUCTURE AND FUNCTION OF LYSOSOMES

Lysosomes are a heterogeneous collection of membrane-bound vesicles and vacuoles that derive from **Golgi complex** vesicles. They contain 50 or more *hydrolytic enzymes,* most being glycoproteins that are active at acid pH, and they stain cytochemically for *acid phosphatase.* Lysosomes are spherical or irregular in shape, with diameters of 0.25-0.8 µm. Present in most cells, they are especially abundant in cells engaged in *phagocytosis.* They serve in defense against infection by engulfing viruses, bacteria, and other pathogens. They are an intracellular digestive system for normal turnover and removal of worn-out organelles in cells. Also, in response to cell injury, they aid *autolysis* of cells—a self-destructive role, which leads to cell death when packaged lysosomal enzymes are released. Newly formed electron-dense **primary lysosomes** have a homogeneous, granular content with no digested material inside. They become **secondary lysosomes,** which are normally larger and more heterogeneous in appearance and electron density. They usually contain remnants of digested material. **Tertiary lysosomes (residual bodies),** the oldest lysosomes, have completed digestive functions and are prominent in long-lived cells such as nerve and cardiac muscle cells. They often have bizarre shapes and are almost entirely filled with debris, including concentric lamellae, indigestible material, and crystalline deposits. They often accumulate *lipofuscin,* a wear-and-tear pigment. Lysosomal membranes contain a unique phospholipid resistant to degradation by lysosomal enzymes, so other cell components are separated from them (Figs.1-10*A* and *B*).