CHAPTER

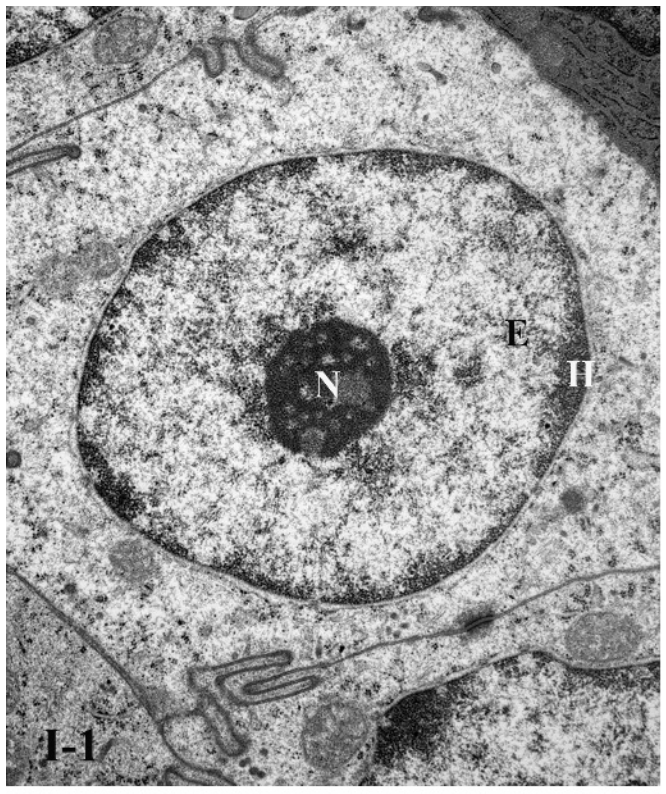
I

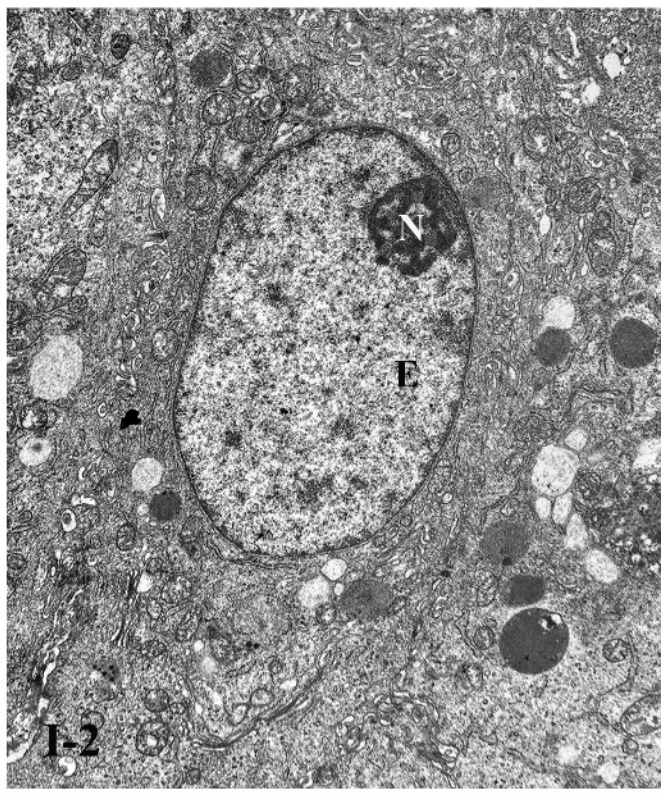
CELLULAR ORGANELLES AND SURFACE SPECIALIZATIONS

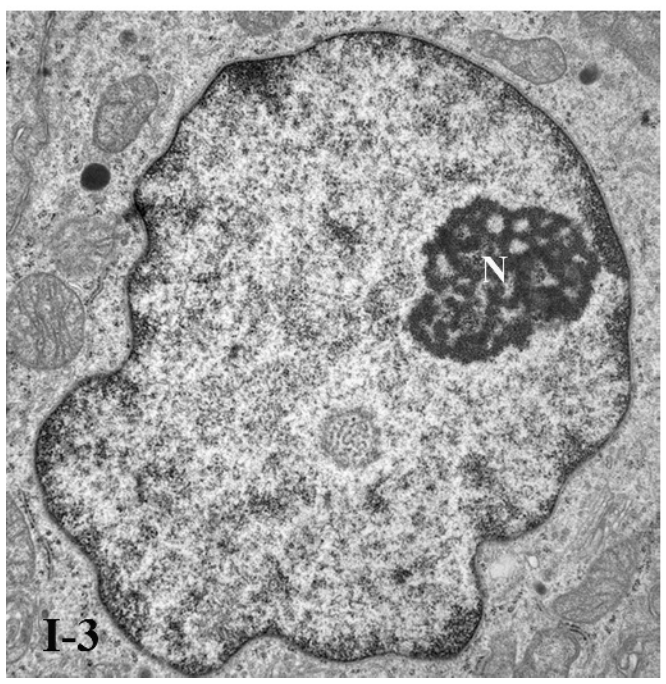
A. NUCLEI AND NUCLEOLI

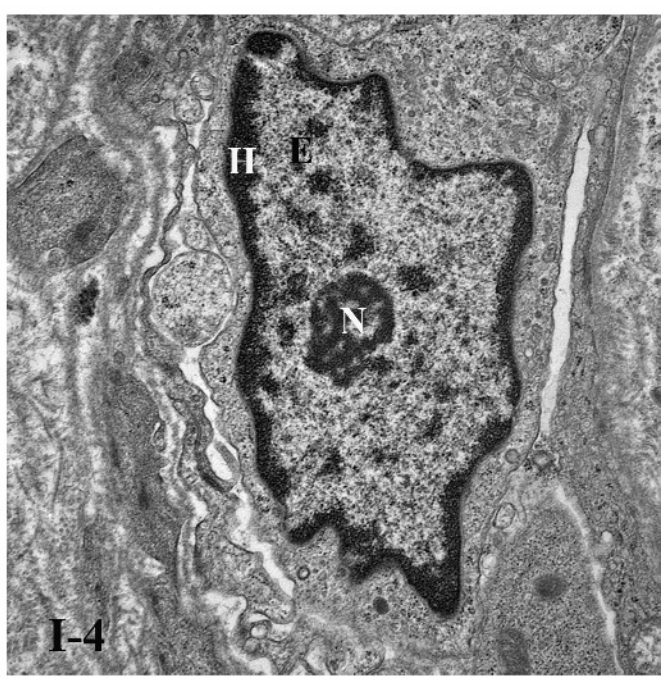
Cell nuclei vary somewhat with regard to size, shape, chromatin pattern, and number among the various types of human tissues, as is shown in the images in this section (Figs. I-1 to I-14). Probably the most common morphology consists of a round to oval shape, with a single eccentric nucleolus, and a mixture of inactive (heterochromatin) and active (euchromatin) DNA. The darker staining heterochromatin is scattered throughout the lighter staining euchromatin, but is often concentrated along the edge of the inner nuclear membrane. The ratio of heterochromatin to euchromatin is often altered with cell maturation and with changes in cellular synthetic activity. While most cells contain a single nucleus, liver cells and myocardial muscle cells often contain two nuclei, skeletal muscle cells are multinucleated (Figs. I-13 and I-14), and red blood cells (Fig. I-10) discard their nuclei at maturity. Nuclei may be indented (Fig. I-11), lobed (Figs. I-10 and I-12), or distorted in shape (Figs. I-8 and I-9) to match the outline of a cell. There is usually one nucleolus in each nucleus, and its size may increase with cellular synthetic activity. The nucleolus appears to be made up of a three-dimensional network of fibrils with which are associated lighter staining regions as well as heterochromatin-like material. DNA within the nucleolus codes for ribosomal RNA and the nucleolus functions in the synthesis and assembly of ribosomal subunits. Ribosomal proteins enter the nucleus and ribosomal subunits formed in the nucleolus leave the nucleus through complex, selective nuclear pores (Figs. I-61 and I-62) in the nuclear envelope.

Ultrastructure Atlas of Human Tissues, First Edition. Fred E. Hossler.

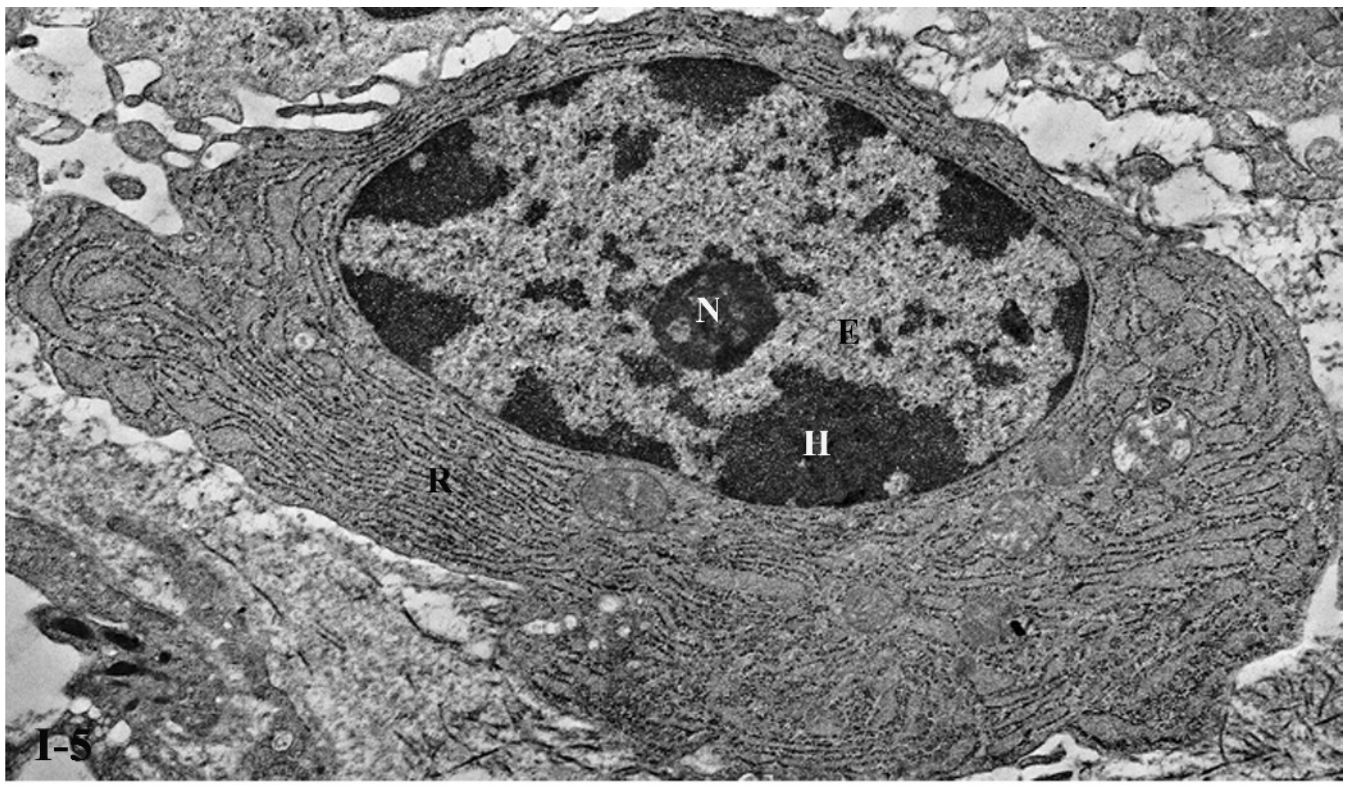


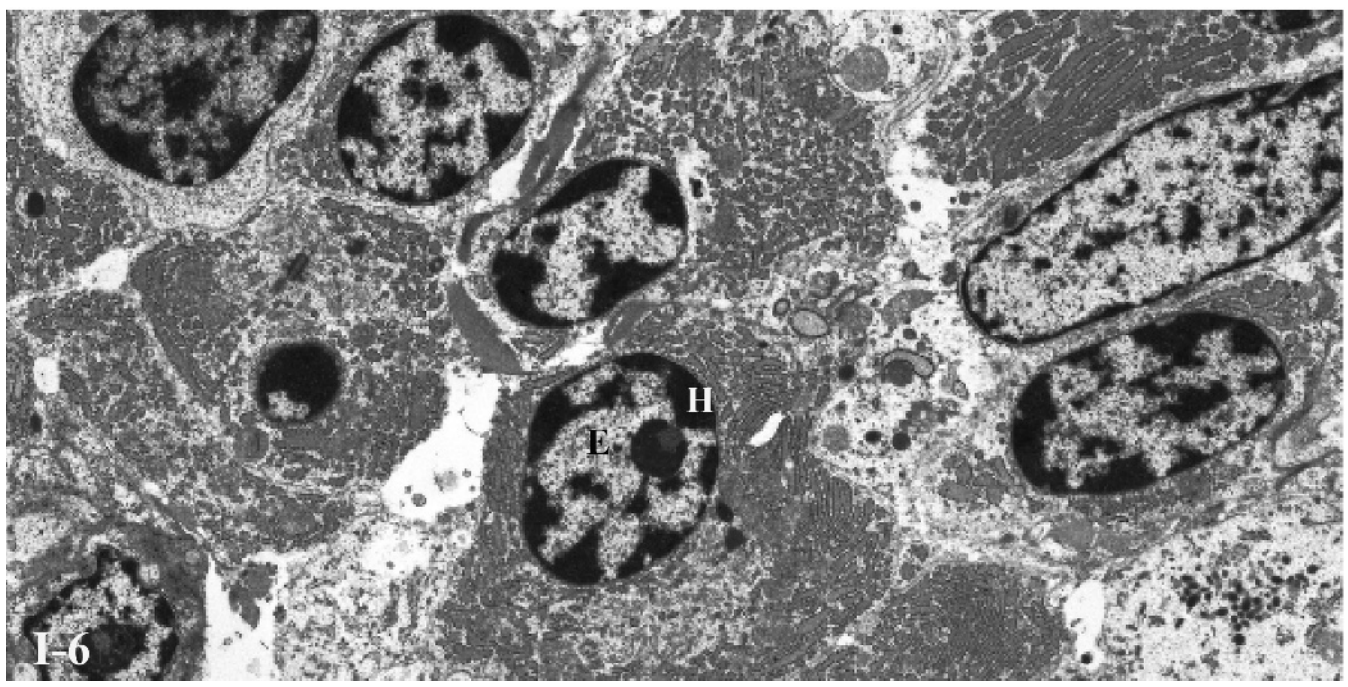




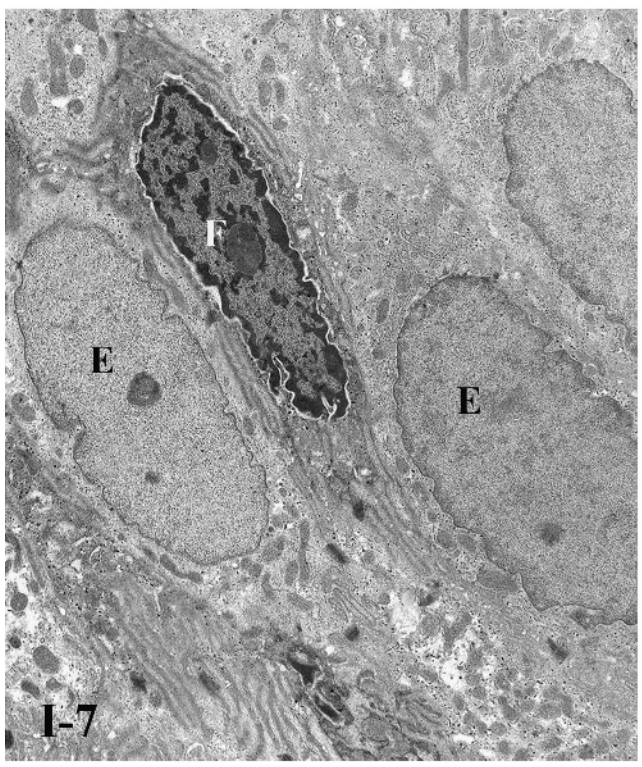


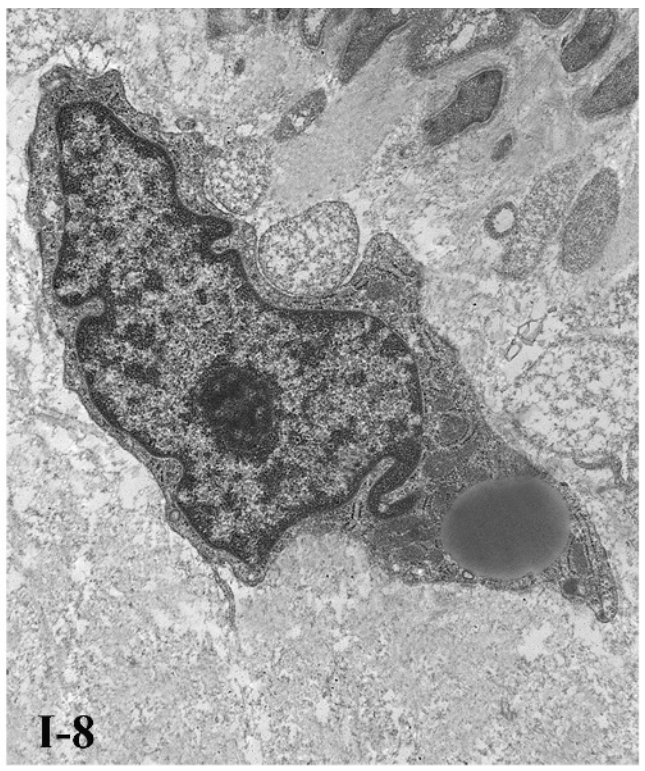
FIGURES I-1 and I-4. I-1 Nucleus of epithelial cell from human jejunum. ×14 167. I-2 Nucleus of cell from human gall bladder. ×8409. I-3 Nucleus (N) of human kidney tubule cell. ×25 000. I-4 Nucleus of fibroblast from human kidney. ×20 521. N, nucleolus; E, euchromatin; H, heterochromatin.

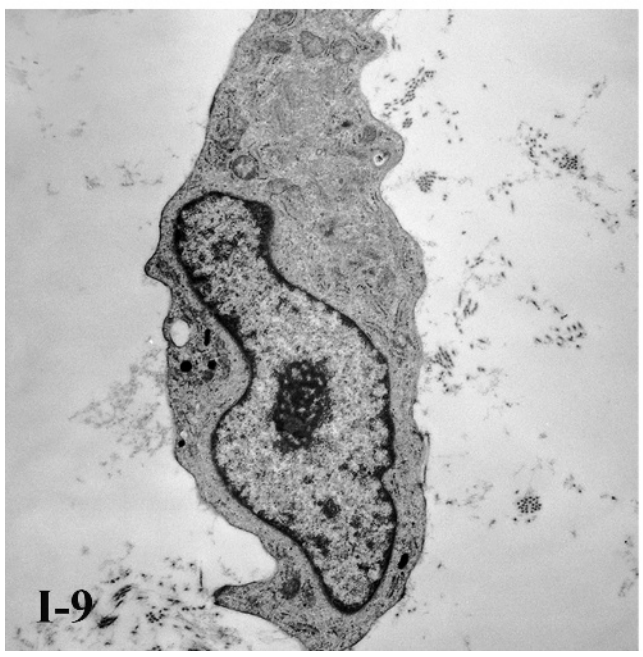


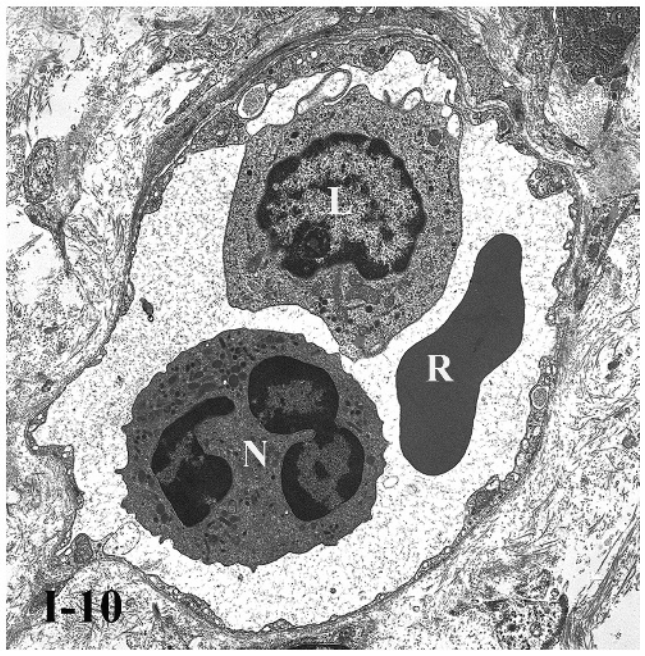


FIGURES I-5 and I-6. I-5 Plasma cell from human colon. Note "spoke wheel" pattern of nucleolus (N) and heterochromatin (H). ×15286. I-6 Plasma cell cluster from human jejunum. Again note peripheral heterochromatin pattern in nuclei. ×2250. E, euchromatin; R, rough endoplasmic reticulum; H, heterochromatin.

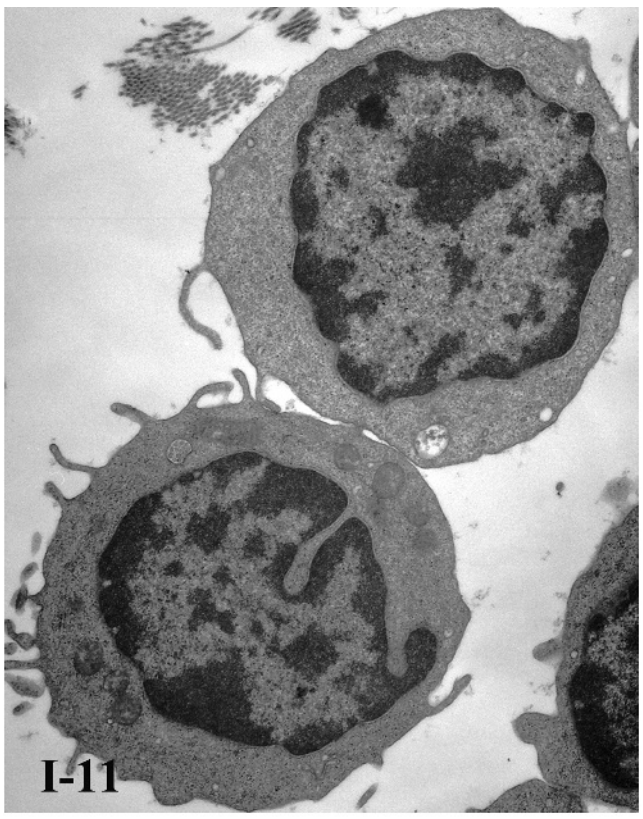


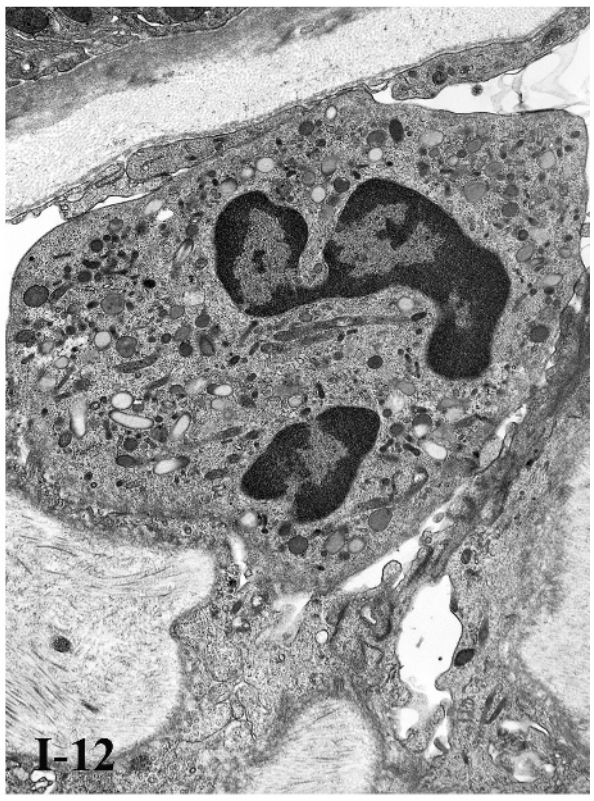


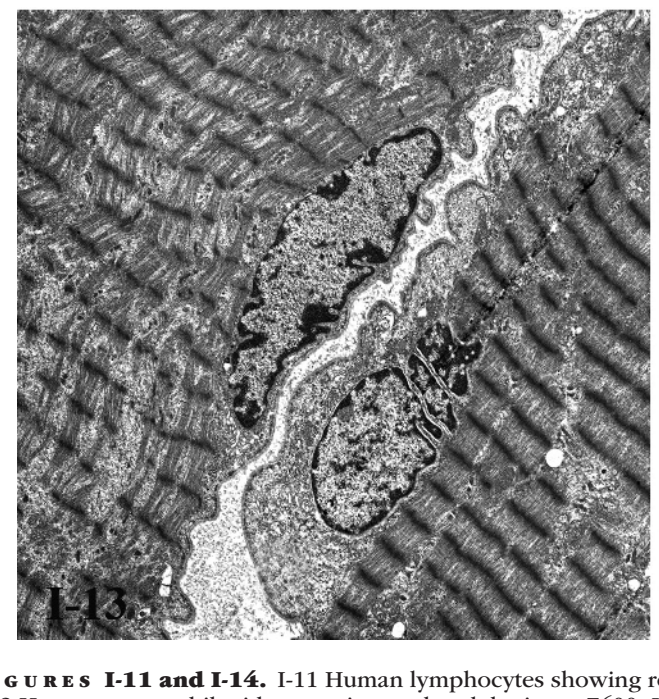


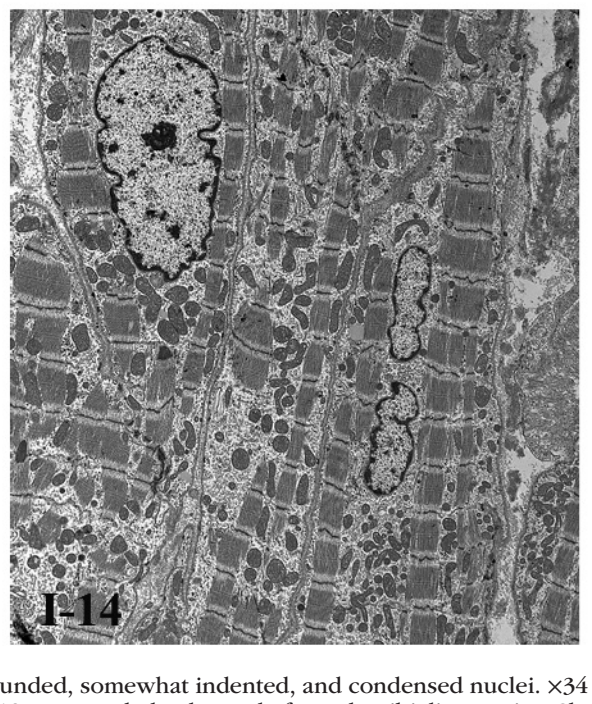


FIGURES I-7 and I-10. I-7 Comparison of nuclei of fibroblast (F) and epithelial lining cells (E) from human colon. I-8 and I-9 Human fibroblasts demonstrating irregular nuclear shapes influenced by cell shapes. ×23 000 and ×21 585. I-10 Cells within a capillary in the wall of the human ureter demonstrate variations in nuclei. The lymphocyte (L) has a somewhat rounded and condensed nucleus, the neutrophil (N), exhibits a highly condensed, multilobed nucleus, while the red blood cell (R) has given up its nucleus. ×15 400.





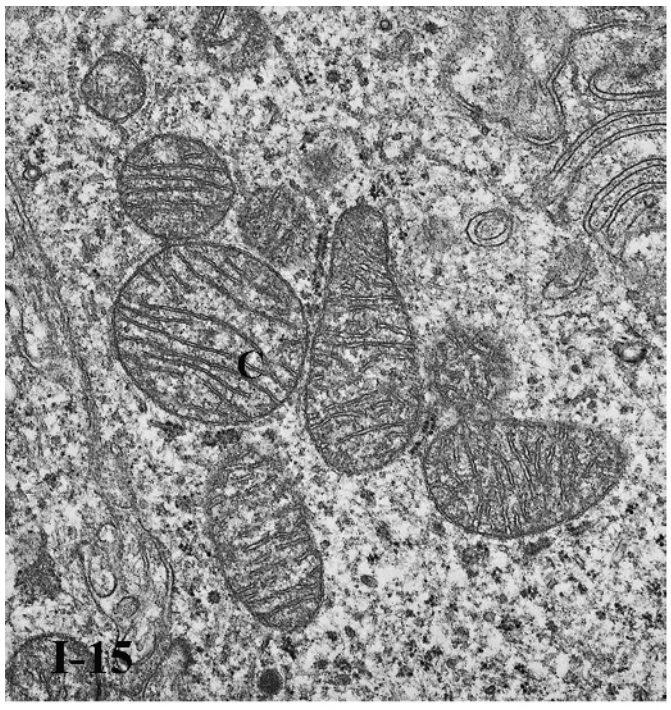


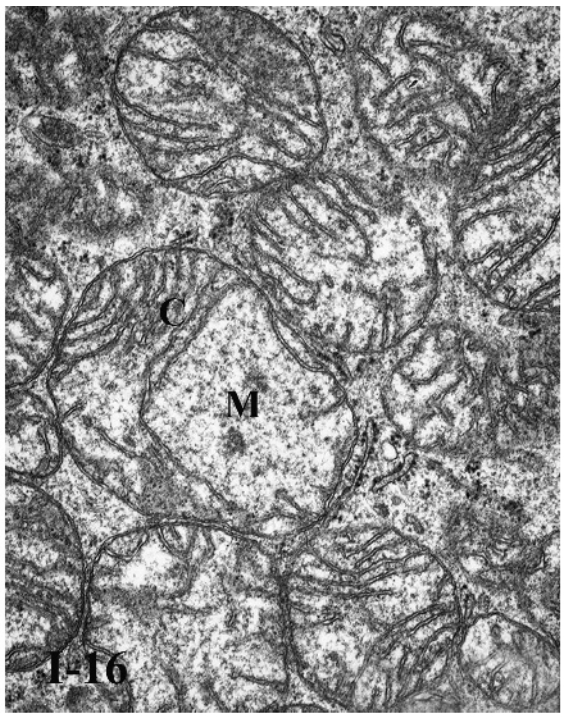


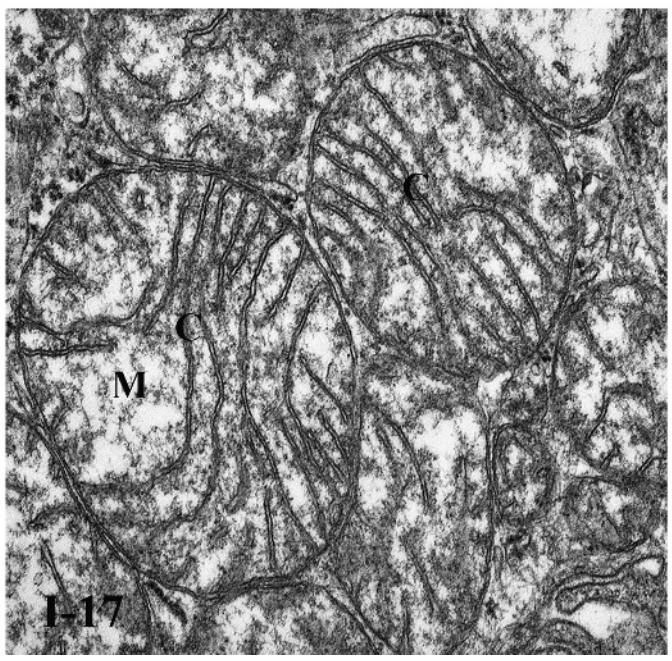
FIGURES I-11 and I-14. I-11 Human lymphocytes showing rounded, somewhat indented, and condensed nuclei. ×34 367. I-12 Human neutrophil with extensive nuclear lobation. ×7600. I-13 Human skeletal muscle from the tibialis anterior. Skeletal muscle cells are multinucleated. Seen here are two adjacent muscle cells, each showing a single nucleus along its periphery. ×5106. I-14 Cardiac myocytes from the human atrium. Cardiac myocytes may contain one or two nuclei. The cell at the right center may have two nuclei or, more likely, the tissue section may have been cut along the edge of a single nucleus. ×5000.

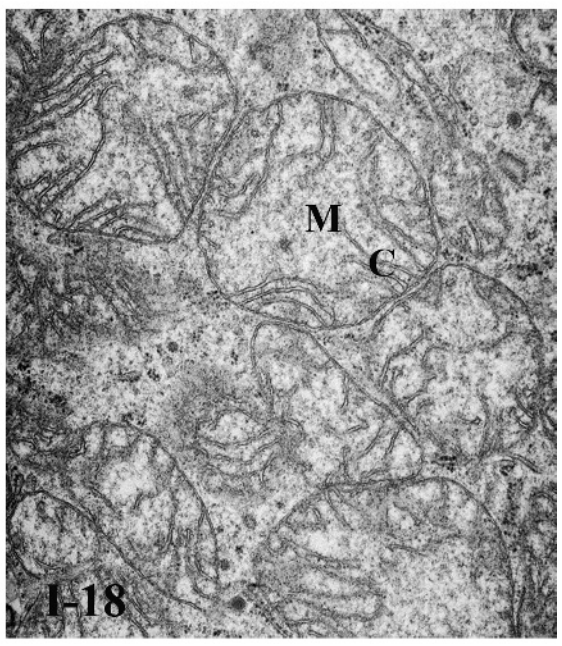
B. MITOCHONDRIA

Like nuclei, mitochondria are bound by a double membrane. Folds in the inner membrane, called cristae, extend toward the interior, or matrix space, of the mitochondrion (Figs. I-15 to I-18). Mitochondria are self-replicating and their matrix space contains its own unique segment of DNA, and unique RNA species (evidence to support the belief that these organelles were originally derivatives of a symbiotic bacterium). The outer membrane contains pores that facilitate the free flow of small molecules. The inner membrane is essentially impermeable and is rich in proton pump enzymes (NADH dehydrogenase complex and cytochrome chain complex), and ATP synthase. Enzymes involved in the citric acid cycle as well as some enzymes involved in fatty acid oxidation are located within the matrix space. This functional relationship between the matrix and the inner membrane defines the primary function of the mitochondrion, ATP synthesis. Because of this basic function, most cells contain mitochondria, but this organelle is especially abundant in synthetically active cells and in cells involved in active transport.





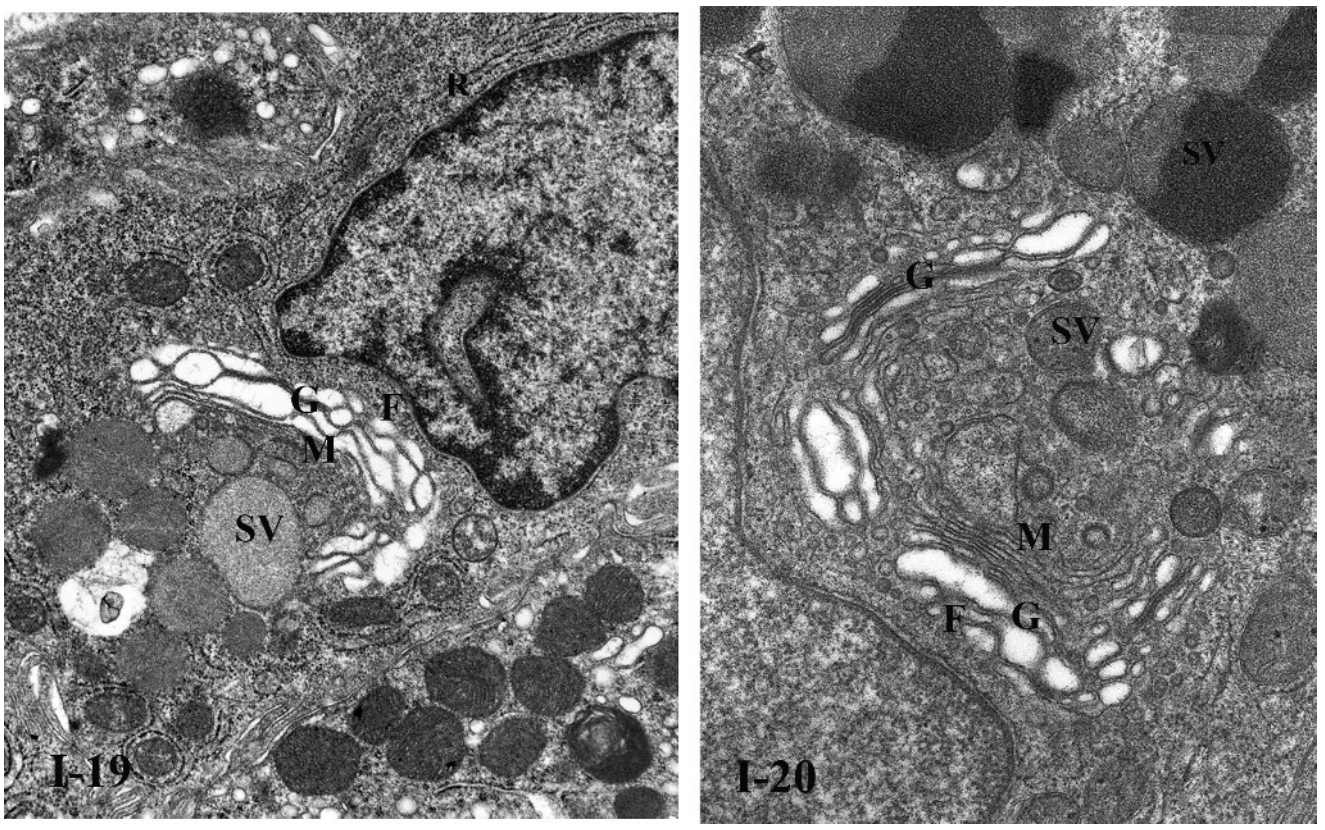




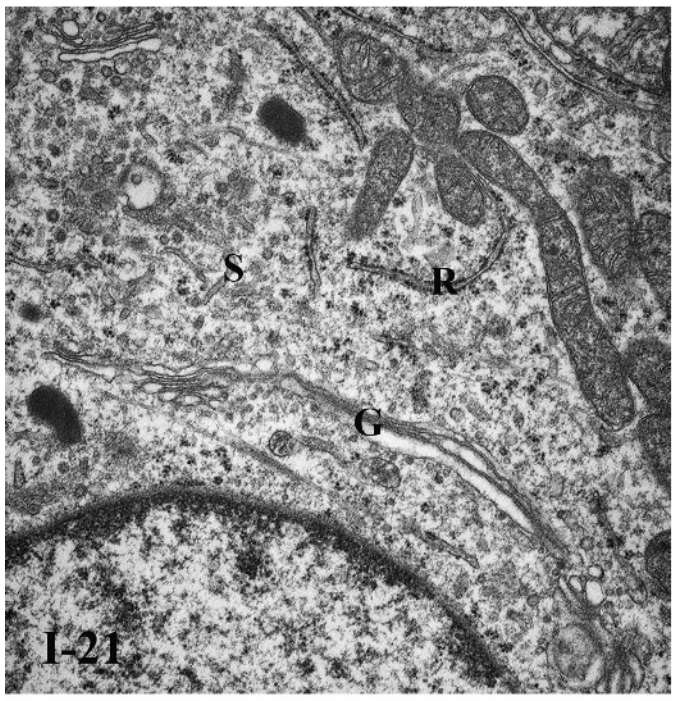
FIGURES I-15 to I-18. Clusters of mitochondria from distal tubule cells in the human kidney. M, matrix space; C, cristae. ×45 625, ×61 818, ×81 820, and ×53 500.

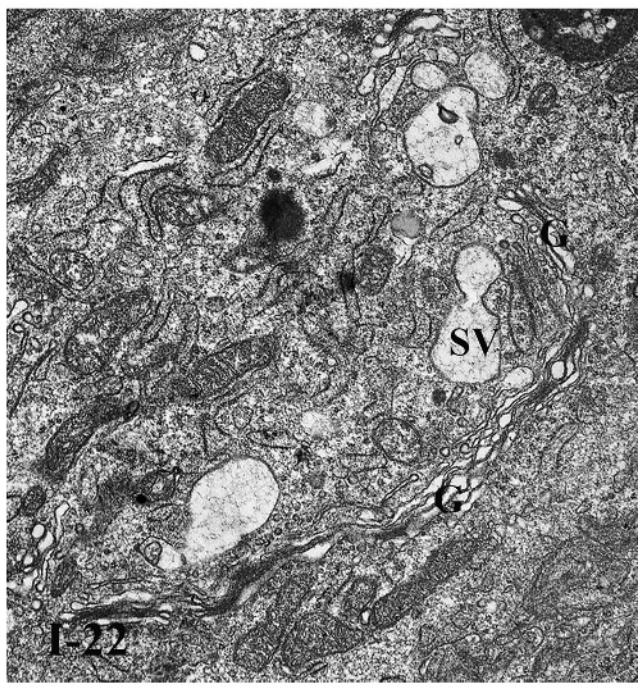
C. GOLGI COMPLEX

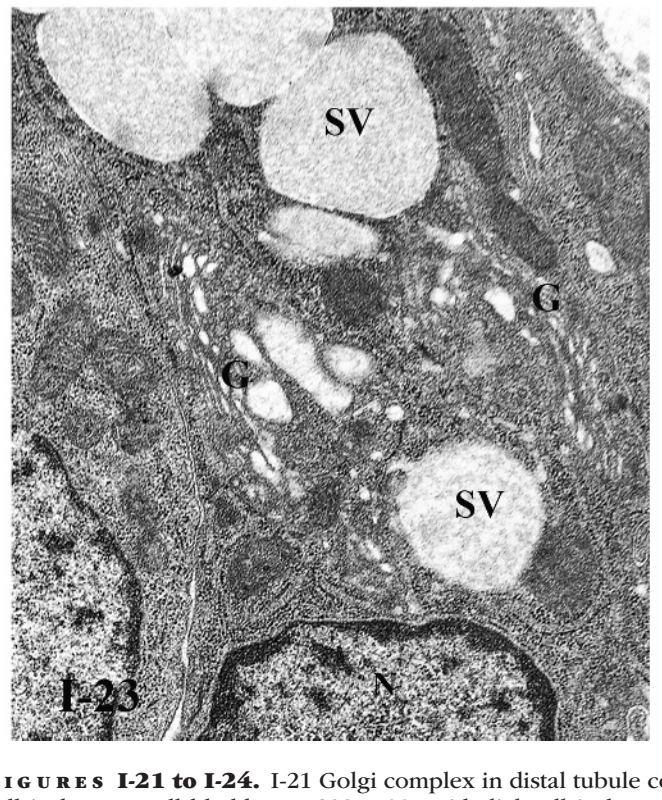
The Golgi complex consists of a stack of flattened membrane vesicles or cisternae (Figs. I-19 to I-24). The stack is usually concave on one side (the forming face or *cis*-face) and convex on the opposite side (maturing face or *trans*-face). The Golgi complex is an essential component in the process of cell secretion and in the movement of membrane vesicles between the cytoplasmic organelles and the cell surface. Most cells contain a Golgi complex, but Golgi complexes are especially well developed and abundant in cells involved in secretion and in lysosome synthesis. In secretory cells the forming face of the Golgi complex is closely associated with rough endoplasmic reticulum (RER) and the maturing face is associated with secretory vesicles. As the secretory proteins pass through the Golgi complex they are sorted, packaged, and chemically modified.

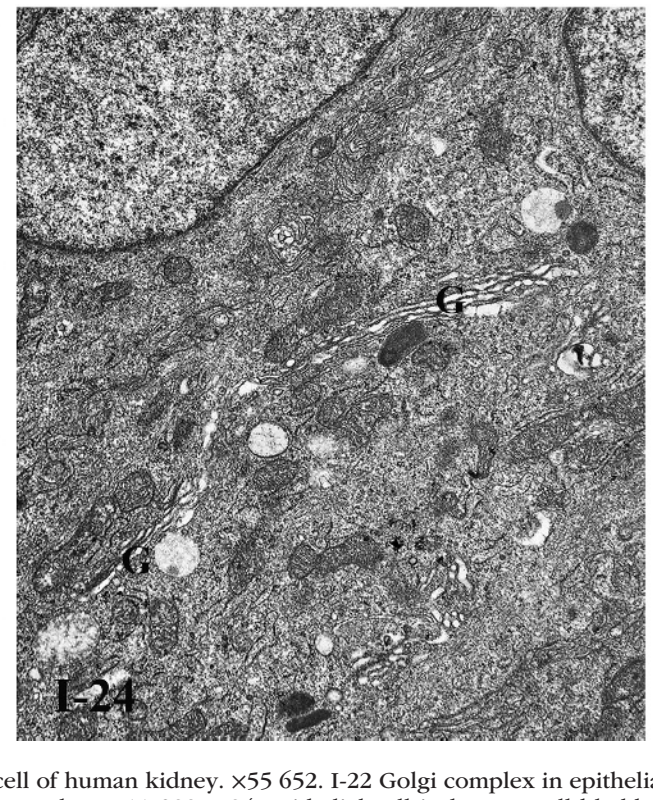


FIGURES I-19 to I-20. I-19 Golgi complex in chief cell of human fundus. ×15 000. I-20 Golgi complex in chief cell of human fundus. ×26 700. G, Golgi complex; F, forming face of Golgi; M, maturing face of Golgi; R, rough endoplasmic reticulum; SV, secretory vesicle.





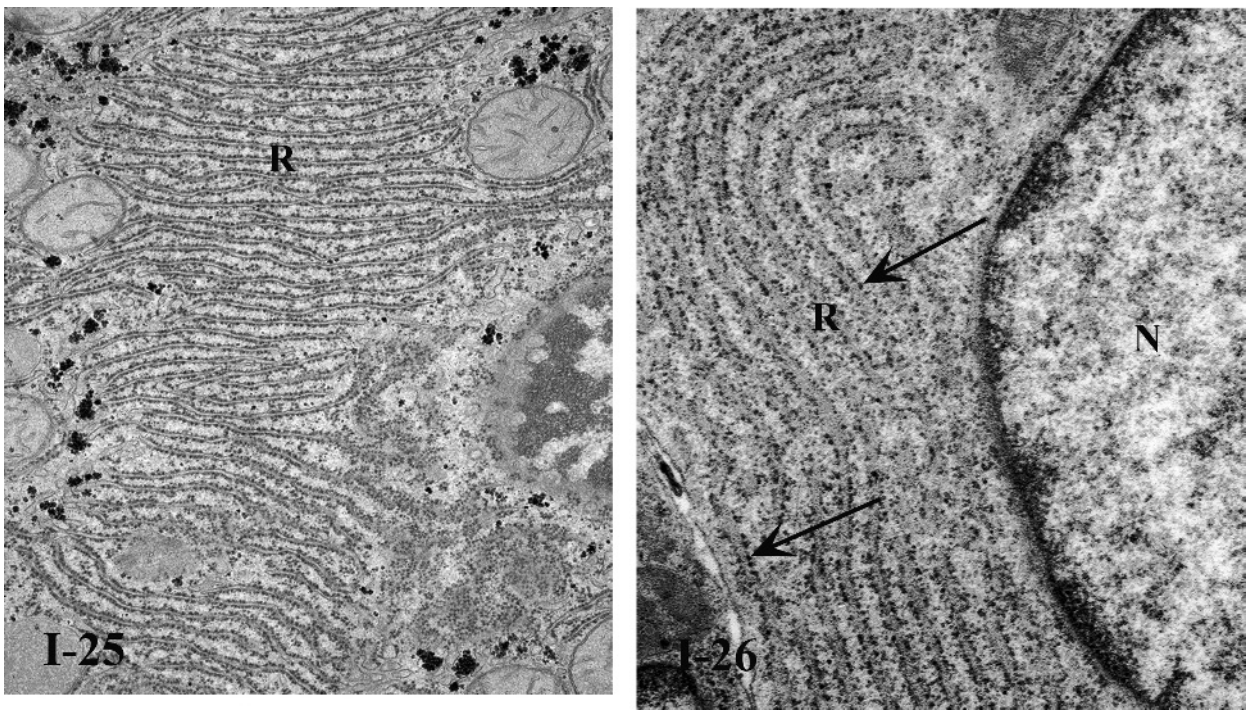




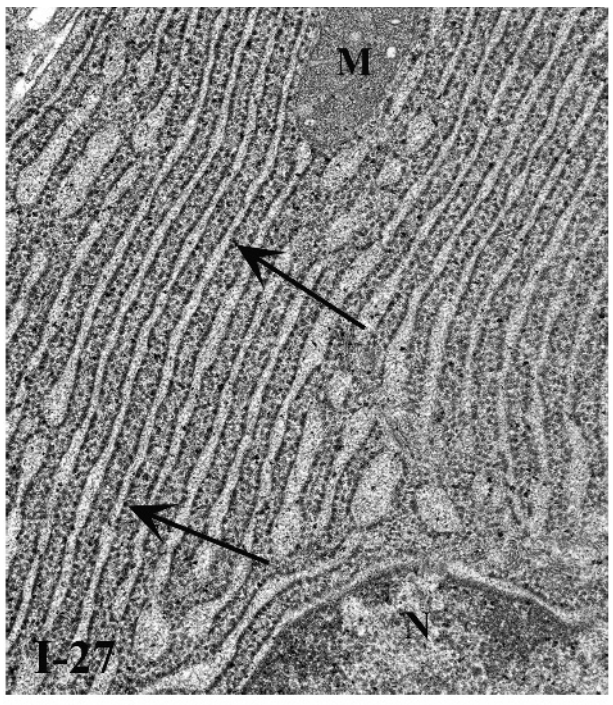
FIGURES I-21 to I-24. I-21 Golgi complex in distal tubule cell of human kidney. ×55 652. I-22 Golgi complex in epithelial cell in human gall bladder. ×7800. I-23 Epithelial cell in human colon. ×11 923. I-24 Epithelial cell in human gall bladder. ×13 000. G, Golgi complex; F, forming face of Golgi complex; M, maturing face of Golgi complex; SV, secretory vesicles; S, smooth endoplasmic reticulum; R, rough endoplasmic reticulum.

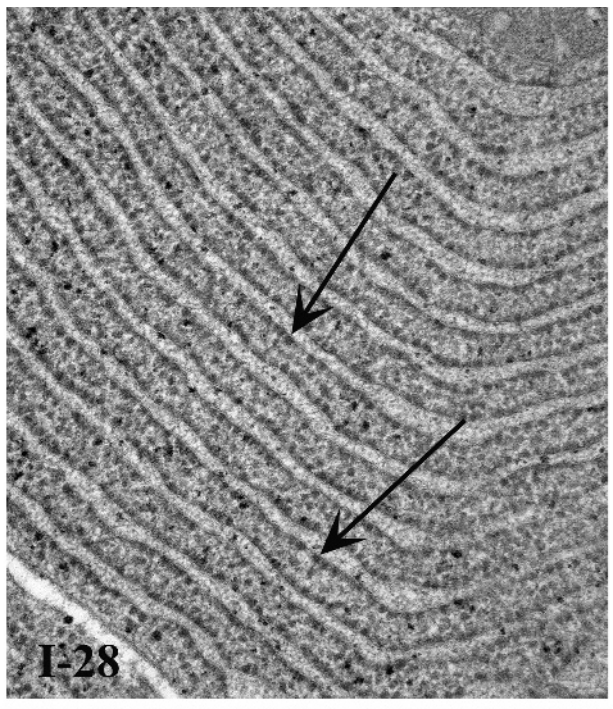
D. ROUGH ENDOPLASMIC RETICULUM AND SMOOTH ENDOPLASMIC RETICULUM

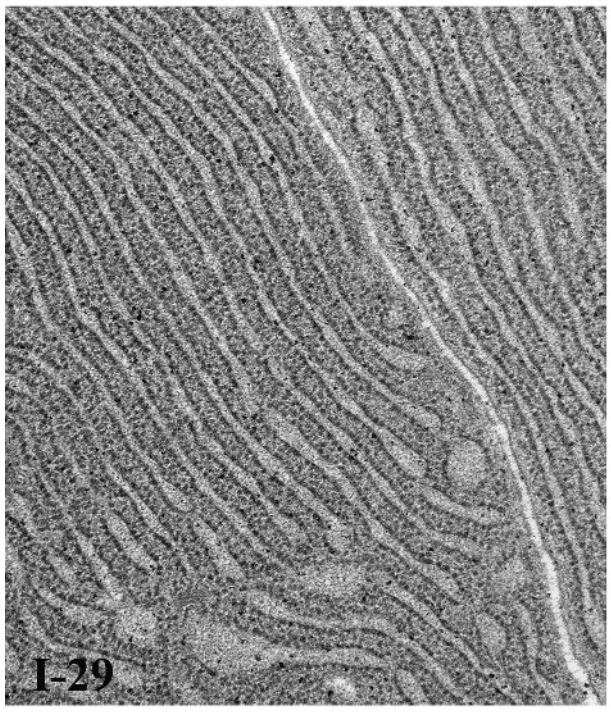
Free ribosomes become involved in protein synthesis when they attach to a messenger RNA and form polysomes. Polysomes within the cell cytoplasm (free polysomes) synthesize proteins for use within the cell. However, when the polysomes are attached to membrane complexes (endoplasmic reticulum) within the cytoplasm, they synthesize proteins for secretion, for incorporation into the cell membrane, or for lysosome formation. Polysomes attached to cytoplasmic membranes are referred to as RER (Figs. I-25 to I-30). When a cell is stimulated to increase its secretory activity, the amount of RER within a cell's cytoplasm can increase dramatically. One example of this is the conversion of a relatively dormant lymphocyte into a plasma cell which then synthesizes and secretes abundant amounts of antibody. Endoplasmic reticulum within the cytoplasm that does not have attached ribosomes is smooth endoplasmic reticulum (SER) (Fig. I-21). SER is less abundant in most cells than RER, but because it is involved in lipid synthesis, steroid synthesis, and drug detoxification, SER is found in liver cells and in endocrine glands. A special form of SER is found in striated muscle cells where it forms complex networks around muscle fibrils and actively sequesters calcium between contractions.

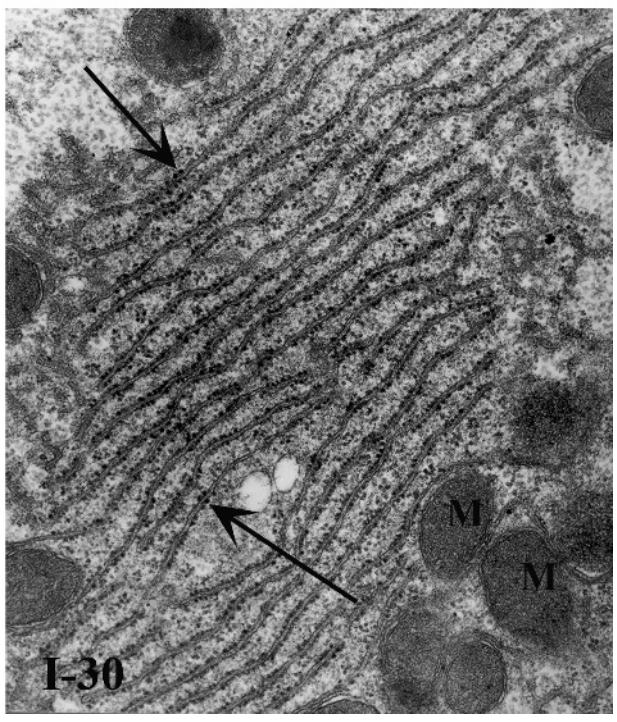


FIGURES I-25 to I-26. I-25 Human hepatocyte. I-26 Epithelial cell in human ileum. N, nucleus; R, rough endoplasmic reticulum; arrows, ribosomes.





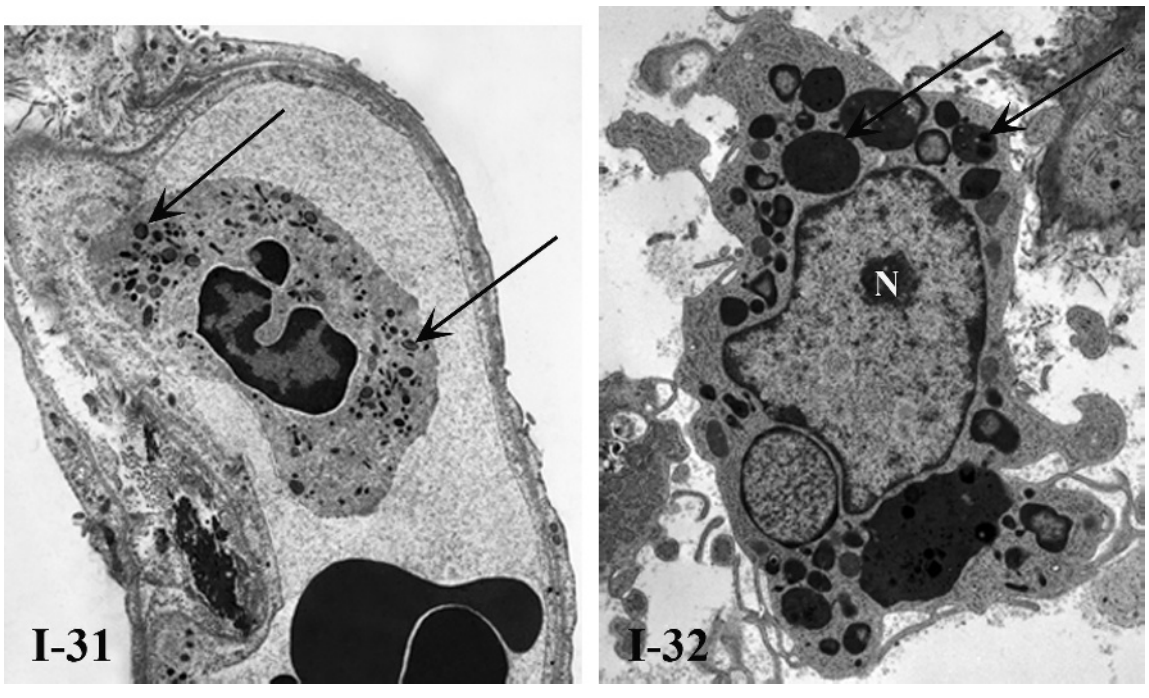




FIGURES I-27 to I-30. I-27 to I-29 Rough endoplasmic reticulum in human pancreatic islet cells. ×40 000, ×50 000, and ×40 000. I-30 Rough endoplasmic reticulum in a human hepatocyte. ×24 000. N, nucleus; M, mitochondria; arrows, ribosomes.

E. LYSOSOMES

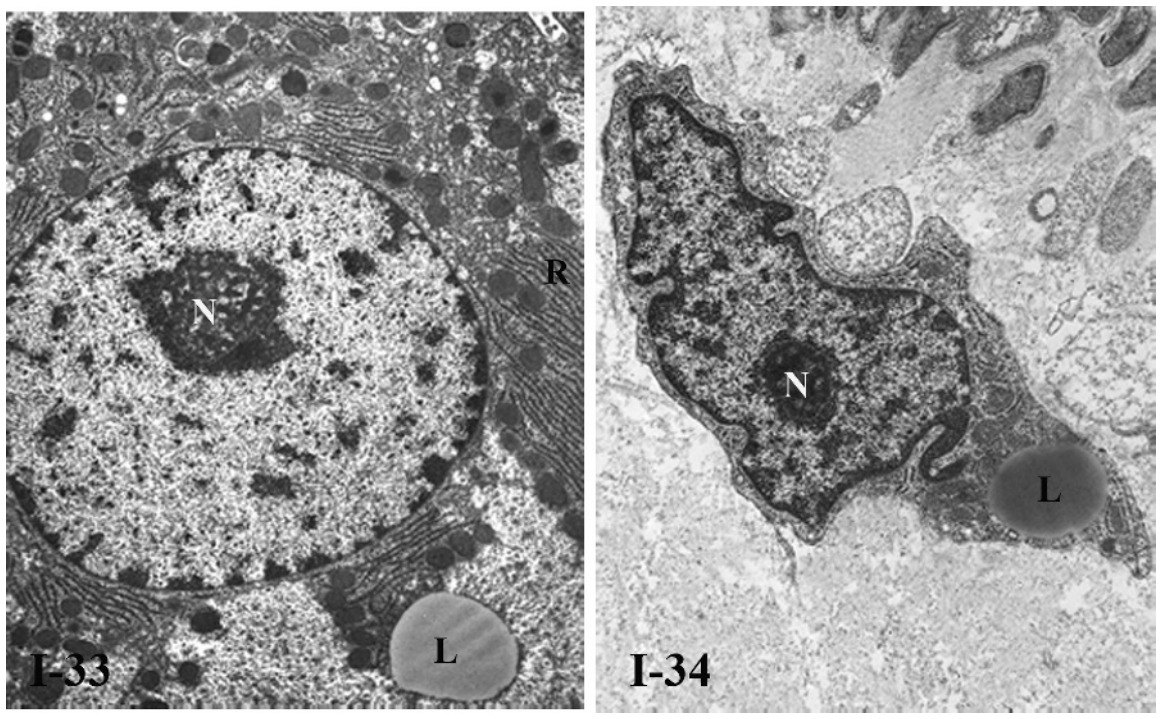
Lysosomes are cytoplasmic membrane-bound vesicles that contain a variety of digestive enzymes, including proteases, lipases, glycosidases, phosphatases, nucleases, and sulfatases (Figs. I-31 and I-32). Proteins destined for lysosomes contain a phosphorylated mannose residue that tags them for delivery into a lysosomal vesicle as they are passed through the Golgi complex. The marker enzyme for lysosomes is acid phosphatase, and most of the enzymes in lysosomes exhibit optimal activity at an acid pH. These organelles are most abundant in neutrophils and macrophages where they are involved in intracellular digestion of phagocytized material such as bacteria or cellular debris. A few specialized cell types release lysosomal granules for extracellular digestive processes. An example of the latter is the osteoclast that is involved in bone remodeling.



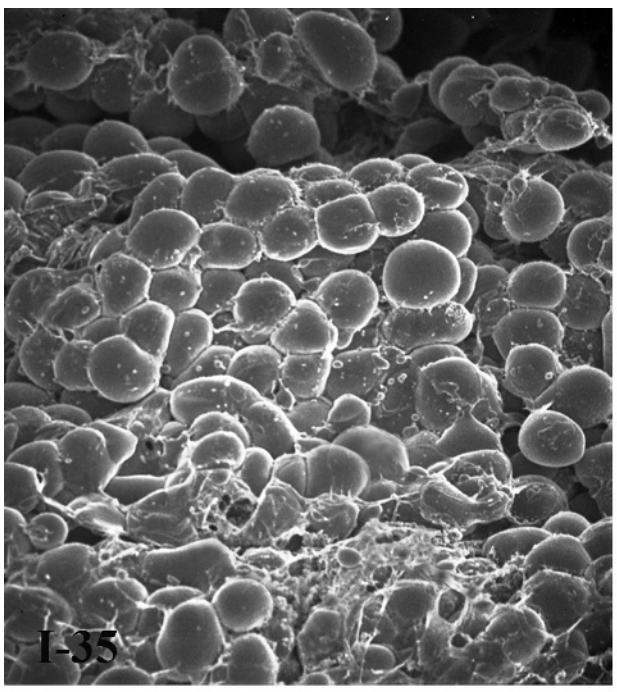
FIGURES I-31 to I-32. I-31 Neutrophil within a capillary in the human lung. ×18 139. I-32 Active macrophage in the lamina propria of the human ileum displaying unusually large lysosomes. ×18 750. N, nucleus; arrows, lysosomes.

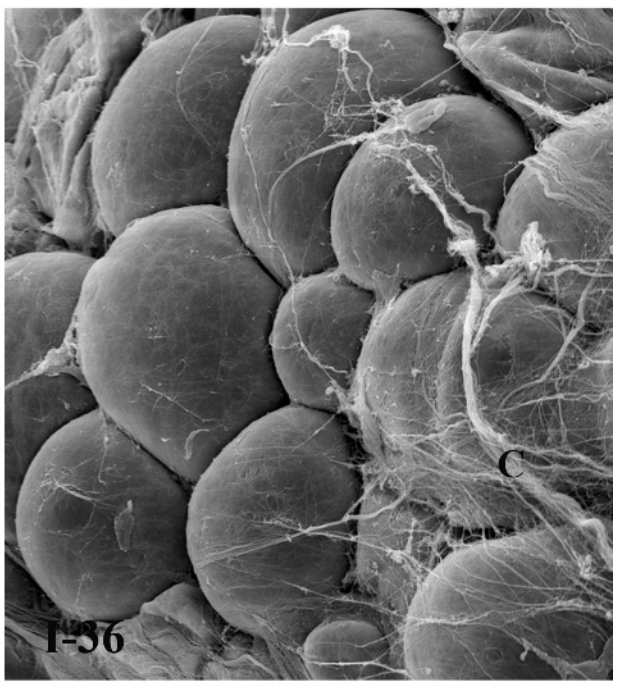
F. CYTOPLASMIC INCLUSIONS

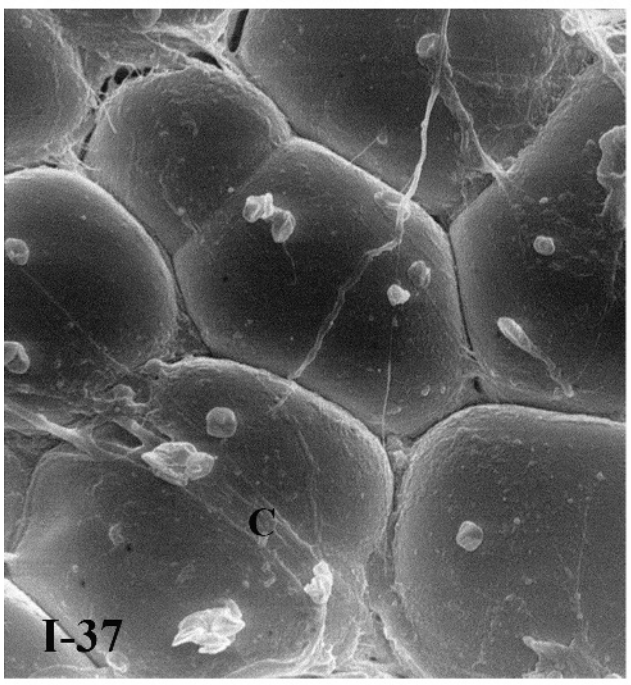
In addition to organelles, some cells include inclusions in their cytoplasm (Figs. I-33 to I-42). Some inclusions function as energy stores while others serve specialized functions. Probably the most readily observed form of energy storage function is evident as lipid storage in adipocytes (Figs. I-35 to I-38) and other cells (Figs. I-33 and I-34), and as glycogen storage in hepatocytes (Figs. I-39 and I-40). Another example of important cytoplasmic inclusions is the melanin pigment granules which the skin keratinocytes ingest as protection against potential ultraviolet radiation damage (Figs. I-41 and I-42).

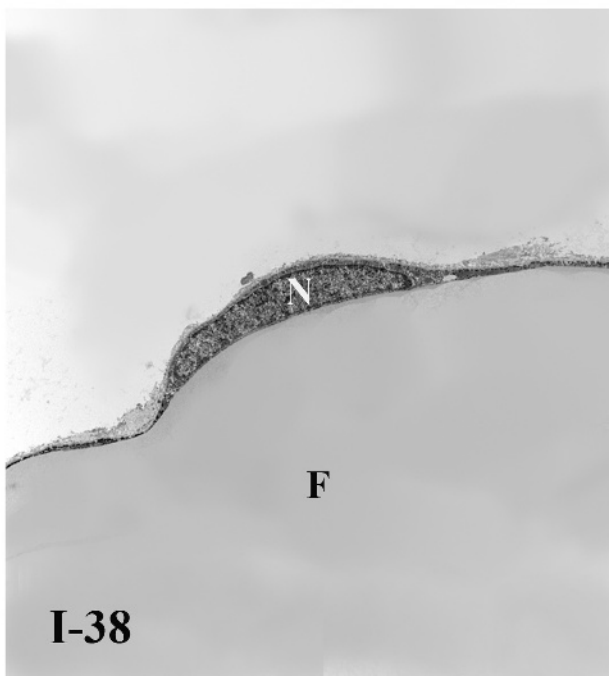


FIGURES I-33 to I-34. I-33 Human hepatocyte. ×6923. I-34 Fibroblast in the lamina propria of the human colon. ×23 000. N, nucleolus; R, rough endoplasmic reticulum; L, lipid droplets.

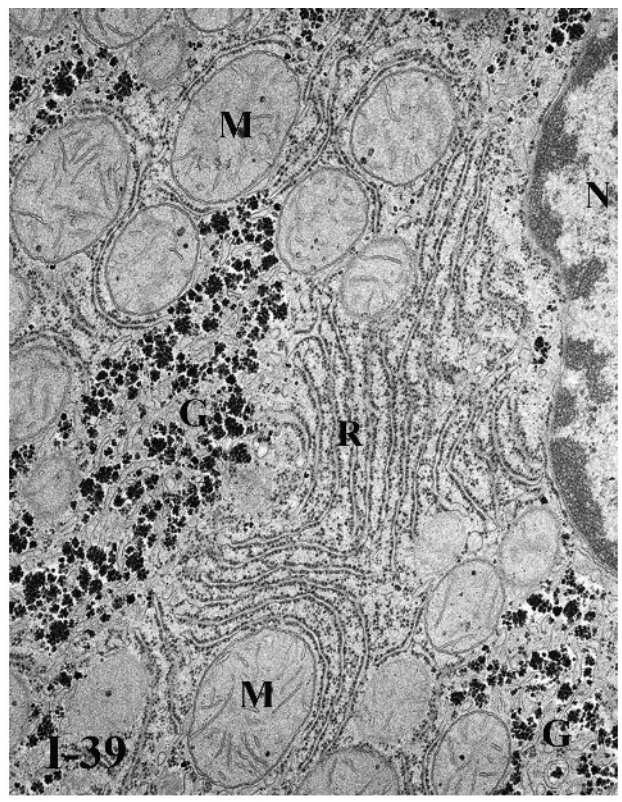


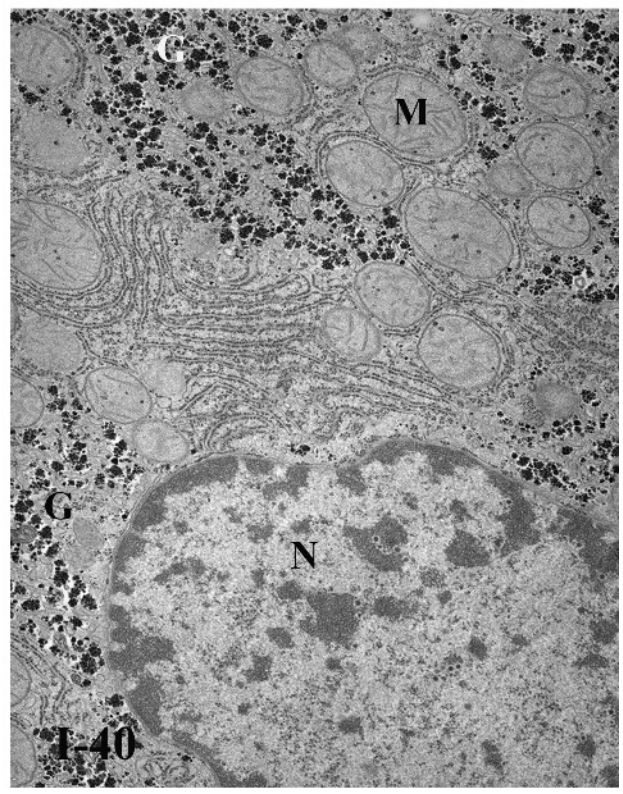


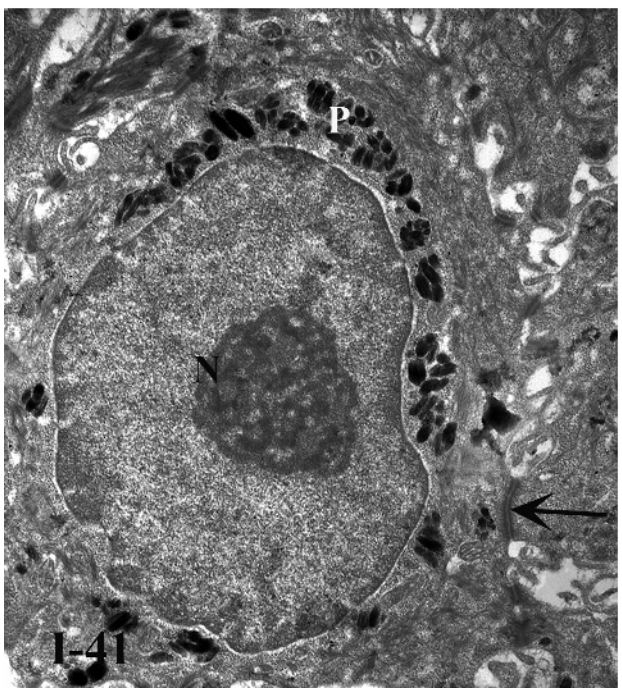


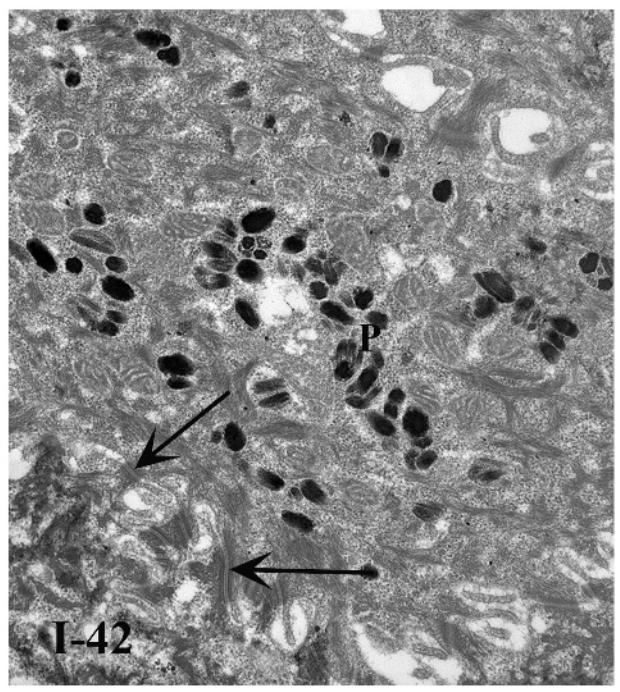


Figures I-35 to I-38. I-35 Adipose tissue from human dermis. ×77. I-36 Fat cells from human dermis. ×500. I-37 Fat cells from human dermis. ×580. I-38 Cross section of edge of a fat cell from human dermis. ×2500. N, nucleus; F, fat deposit; C, collagen fibrils.









FIGURES I-39 to I-42. I-39 Human liver cell. I-40 Human liver cell. I-41 Keratinocyte from human skin. ×11 600. I-42 Details of cytoplasm of keratinocyte from human skin. ×16 000. G, glycogen; M, mitochrondria; R, rough endoplasmic reticulum; N, nucleus; P, melanin granules; arrow, desmosome.

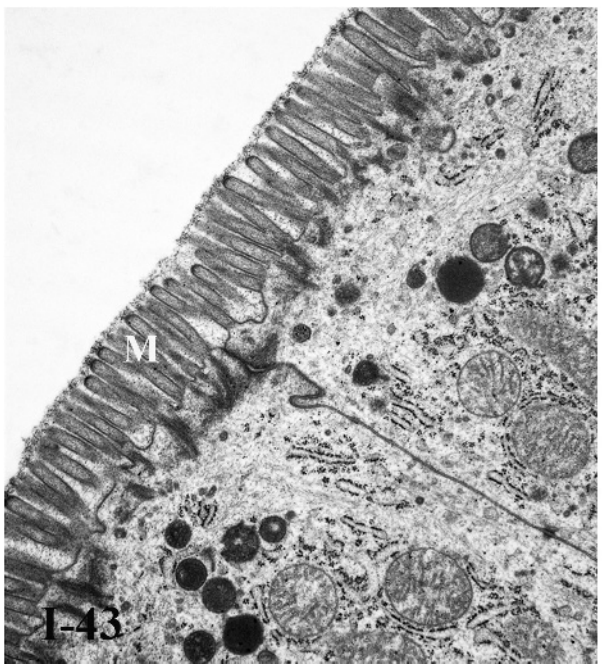
G. PLASMA MEMBRANE JUNCTIONS

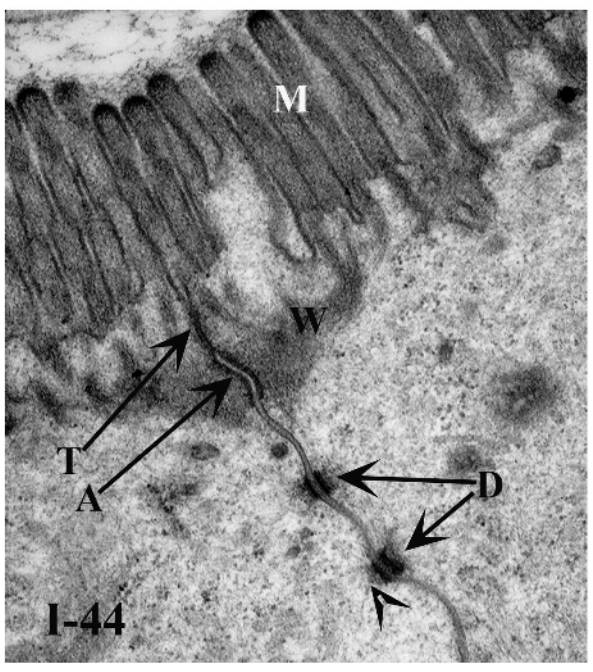
Specialized cell membrane junctions are essential to anchor cells in place, to bind cells together, to permit cell-to-cell communication, or to form seals between adjacent epithelial cells to create apical and baso-lateral domains. Many of the specialized cell junctions are seen in epithelia because of the need for epithelial integrity, a secure permeability barrier, and cell-to-cell communication. For example, a sequential series of junctional complexes is observed between adjacent simple columnar epithelial cells in the intestines. Beginning near the luminal apices of the cells are two sequential belt-like junctions that encircle the entire cell apices (Figs. I-43 to I-45). First is a tight junction (zonula occludens), then an adhering junction (zonula adherens). These two belt-like complexes are followed variably and randomly by two spot-like junctions, a desmosome (Figs. I-43 to I-48) and a gap, or communicating, junction.

The tight junction is formed by the fusion of membrane proteins, claudins, and occludens in the opposing cell membranes, and creates a seal between the luminal space of the intestine and the intercellular space of the epithelial cells. The second belt-like junction, the adhering junction is formed by binding together of membrane proteins, called cadherins, in the opposing cell membranes. The cytoplasmic ends of the cadherin proteins bind to a mesh of actin fibers (called terminal web; Figs. I-44 and I-45) in the cytoplasms of the cell apices. The adhering junctions thus provide structural support to the cell apices.

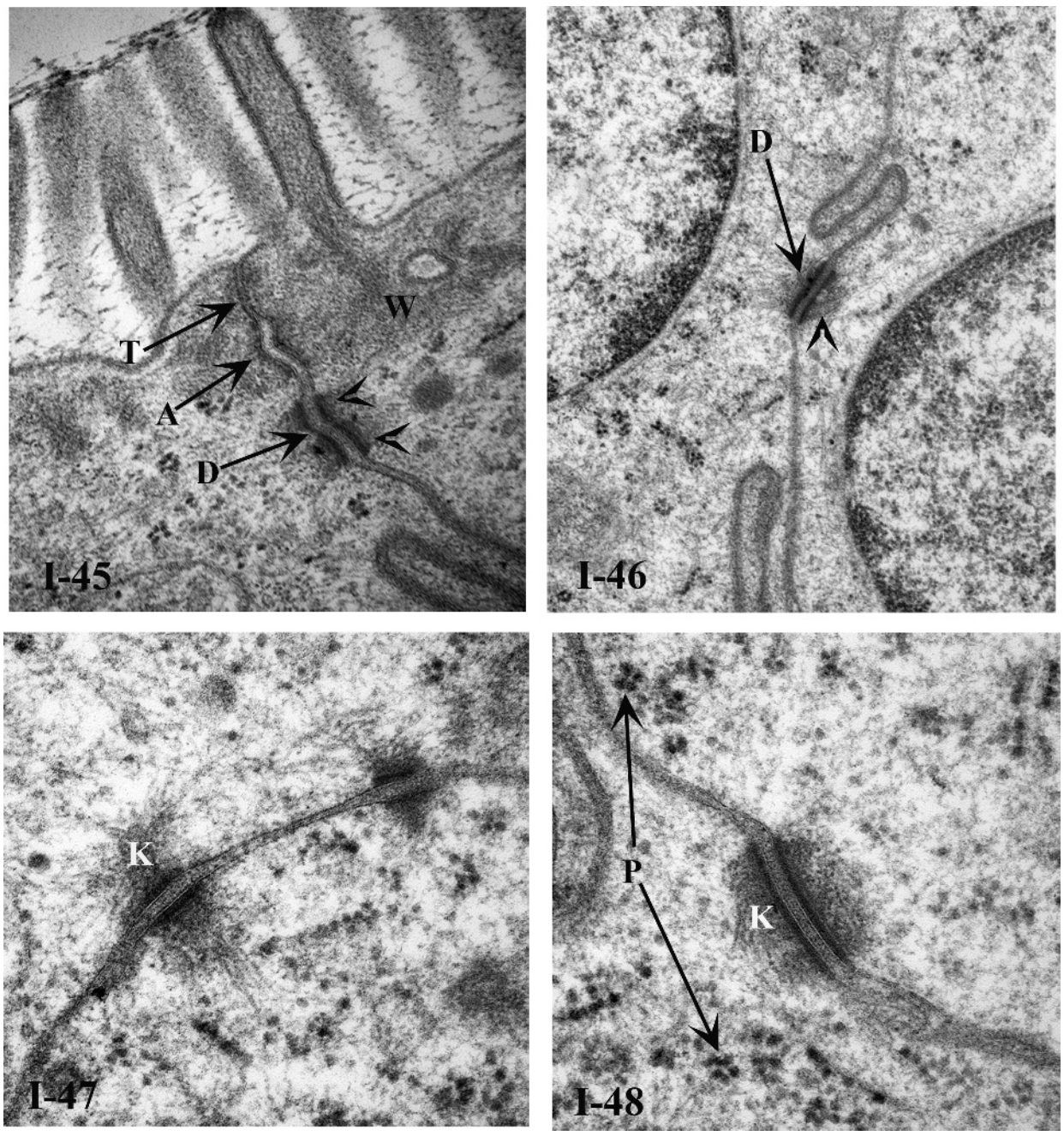
The desmosome also involves cell-to-cell binding via a type of cadherin, but the cytoplasmic end of the cadherins in this case bind to keratins (Figs. I-44 to I-48) that are components of the cytoskeleton of the cell. Desmosomes thus provides very strong "spot welds" which hold adjacent cell together (Figs. I-46 to I-48). At the basal surface of the epithelial cells, cell membrane proteins called integrins bind the cytoplasmic keratins to extracellular proteins laminin and collagen IV, components of the basement membrane.

These basal junctions are called hemidesmosomes. Gap junctions (communicating junctions), the second spot-like junction, involve hexomeric membrane proteins called connexons. Connexons are composed of subunits called connexins that are arranged in a ring to form an adjacent cell; the two pores create an open channel between the cytoplasms of the cells, and allow the exchange of ions and small molecules, as well as electrical conductivity. Gap junctions involve tightly packed arrays of these connexons. Opening and closing of the pores in the connexons is carefully controlled by pH and the concentration of free calcium ions in the cell cytoplasm. Such control is important in preventing the spread of cell damage in the event that an adjacent cell is disrupted. Electrical conductivity is essential for coordinated contractions in smooth muscle and cardiac muscle, and some examples of gap junctions are shown in the chapter on muscle tissues (Chapter IV. Muscle Tissues, Figs. IV-59 to IV-62).





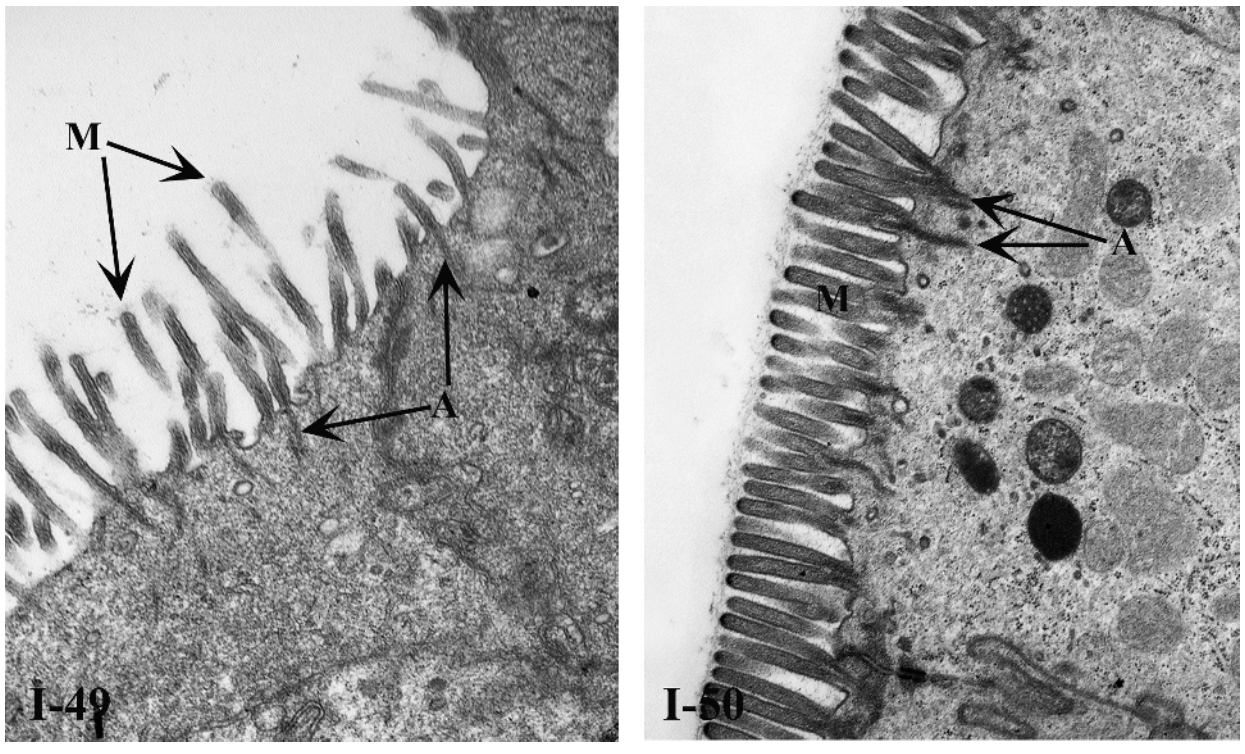
FIGURES I-43 to I-44. I-43 Apical junction between two epithelial lining cells in the human jejunum. ×39 000. I-44 Apical junction between two epithelial lining cells in the human jejunum. ×92 308. A, adhering junction; D, desmosomes; M, microvilli; T, tight junction; W. terminal web.



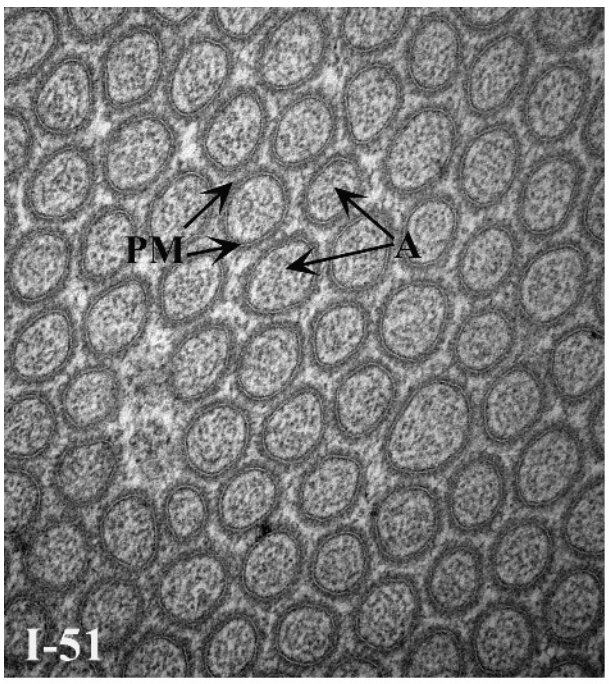
FIGURES I-45 to I-48. I-45 Details of the junctional complex at the apical borders of two epithelial cells in the human jejunum. ×173 077. I-46 A desmosome along the lateral borders of two epithelial cells in the human jejunum. ×133 000. I-47 Two desmosomes joining the adjacent lateral plasma membranes of two epithelial cells in the human jejunum. ×73 000. I-48 Desmosome joining the adjacent lateral plasma membranes of two epithelial cells in the human jejunum. ×74 193. A, adhering junction; D, desmosome; T, tight junction; K, keratin filaments; P, free polysomes; W, terminal web; arrowheads, keratin filaments.

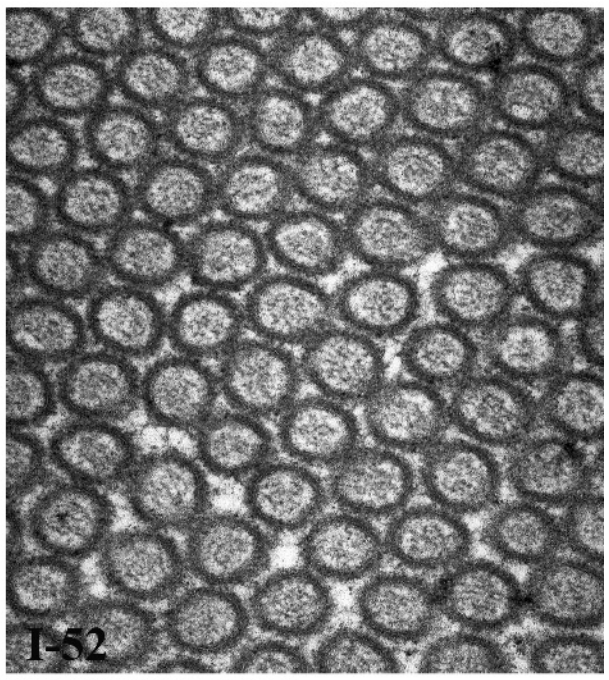
H. MICROVILLI

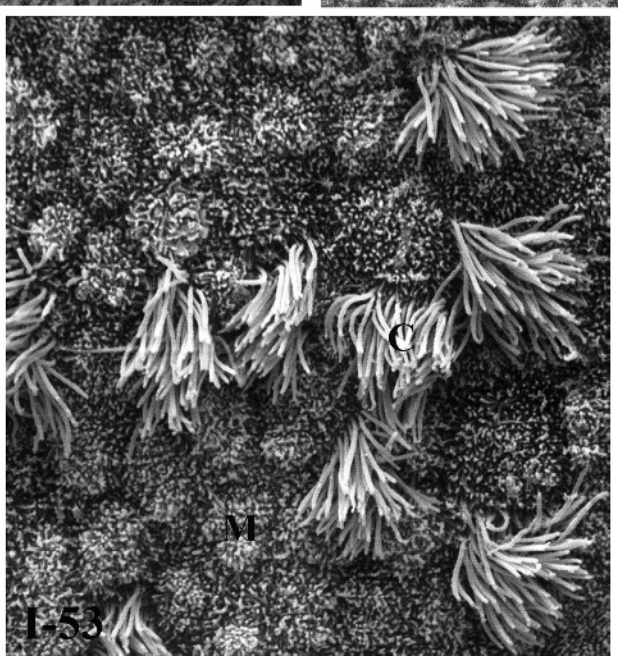
Another mechanism for increasing cell surface area is to provide finger-like projections of the plasma membrane, called microvilli (Figs. I-43 to I-45, Figs. I-49 to I-53; Stereo Pairs I-69 to I-71). The apical surfaces of most epithelial cells exhibit microvilli of varying length, number, and arrangement. In cells actively involved in absorption, such as those lining the proximal tubule of the kidney or those lining the intestines, the microvilli are highly abundant, regularly arranged, and uniform in size. In these cases the microvilli are referred to as the brush border or striated border, and measure about I-5 μm in length and 80 nm in diameter. Microvilli in the intestines are supported by a core of actin filaments (Figs. I-43, I-44, I-49, and I-50) that are attached to the plasma membrane and extend into the apical cytoplasm of the cell where they are anchored to a transversely oriented mass of actin filaments known as the terminal web (Figs. I-44 and I-45). As described above, the terminal web is bound to the lateral cell membrane at the zonula adherens junction (Figs. I-44 and I-45).



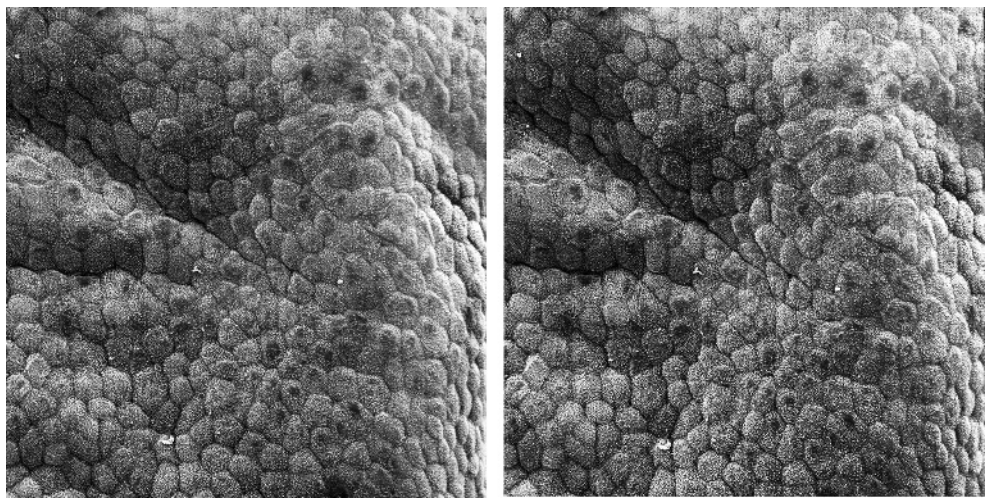
FIGURES I-49 to I-50. I-49 Microvilli on the apical surface of an epithelial cell in the human gall bladder. ×20 100. I-50 Microvilli (brush border) on the surface of the epithelial lining of the human jejunum. M, microvilli; A, actin core of microvilli.



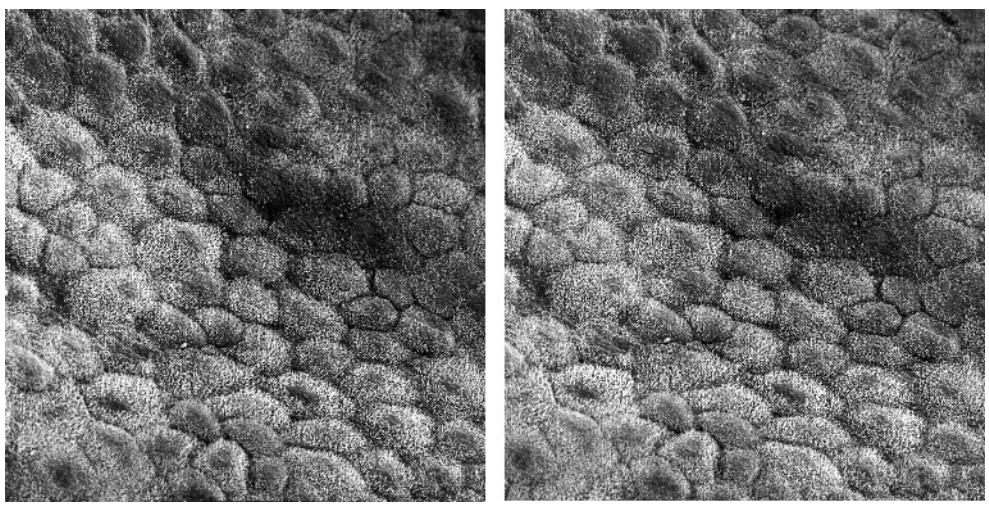




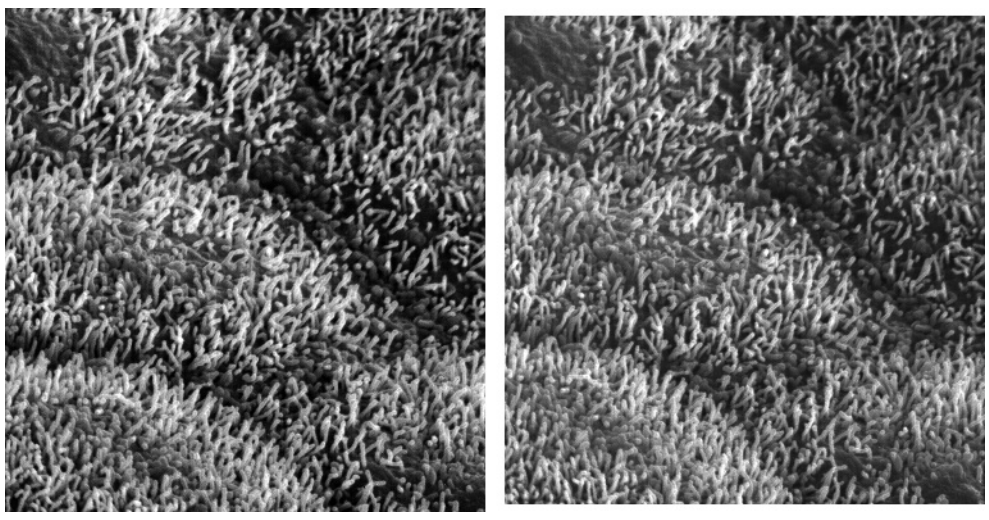
FIGURES I-51 to I-53. I-51 Cross section of microvilli (brush border) on absorptive cells of human jejunum. ×76 023. I-52 Cross section of microvilli (brush border) on absorptive cells of human ileum. ×66 667. I-53 Surface of lining epithelium of human endometrium. ×3000. A, actin core of microvilli; PM, plasma membrane; C, cilia; M, microvilli.



Stereo Pair I-69. Surface of human mesentery in the region of the ovary/oviduct. Note mesothelial cells.



Stereo Pair I-70. Details of surfaces of mesothelial cells seen in Stereo Pair I-69.



Stereo Pair I-71. Details of surfaces of individual mesothelial cells showing abundant microvilli.

I. CILIA AND CENTRIOLES

Cells which are specialized for fluid or mucous transport across their surfaces have cilia on their free surfaces (Figs. I-53–I-60; I-63–I-66; III-28, 31a, 33). Cilia are motile, tubular extensions of the plasma membrane which measure about 7–10 μm in length and 0.25 μm in diameter. They are supported by a highly organized core of microtubules. The microtubule arrangement consists of a ring of nine doublets surrounding two single central microtubules (Figs. I-57 to I-60). This 9 + 2 arrangement, characteristic of motile cilia, is termed an axoneme. One of each of the doublets, designated microtubule A, consists of a ring of 13 tubulin protofilaments, the other, designated microtubule B, is composed of 10 protofilaments but shares 3 of the protofilaments from microtubule A. Two arms, consisting of the motor protein dynein (Figs. I-59 and I-60), extend from the A microtubule of each doublet toward the B microtubule of the adjacent doublet. Ciliary motion results when the dynein arms of the A microtubule utilizes energy from ATP to "crawl" along the B microtubule of the adjacent doublet. The 9 + 2 arrangement of microtubules extends into the apical cell cytoplasm where it changes into a basal body, consisting of a ring of nine triplet microtubules (Figs. I-55 to I-57). The nine doublets are replaced by nine triplets and the central pair of microtubules disappears. The basal body thus resembles the structure of a centriole (Figs. I-61 and I-62). Centrioles are believed to replicate to produce procentrioles that migrate to the cell apex and are the origin of the basal body and cilium. Many epithelial cells (and some nonepithelial cells) display a single central cilium which is nonmotile, and usually lacks the central pair of microtubules in a typical axoneme. These single central cilia have been observed in kidney tubules (Figs. I-63 and I-64), the lining of the oviduct (Fig. I-65) and uterus, thyroid follicles (Fig. I-66), the rete testis, the ducts of glands, and at numerous other sites. It is speculated that these cilia may have a sensory function, or may have been involved in tissue orientation during development (see Figs. III-28, 31A, and 33).

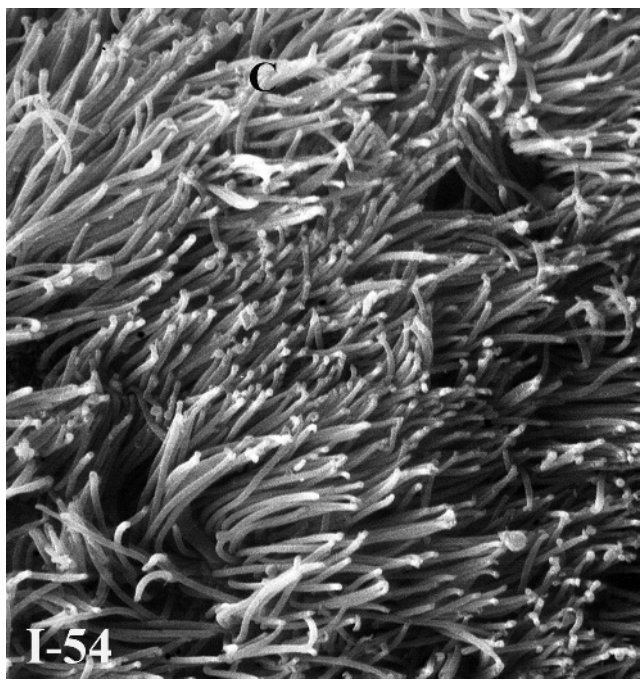
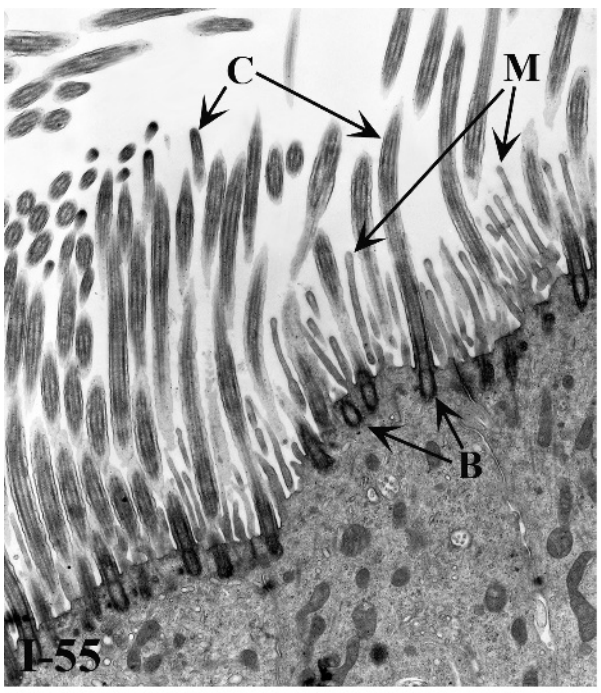
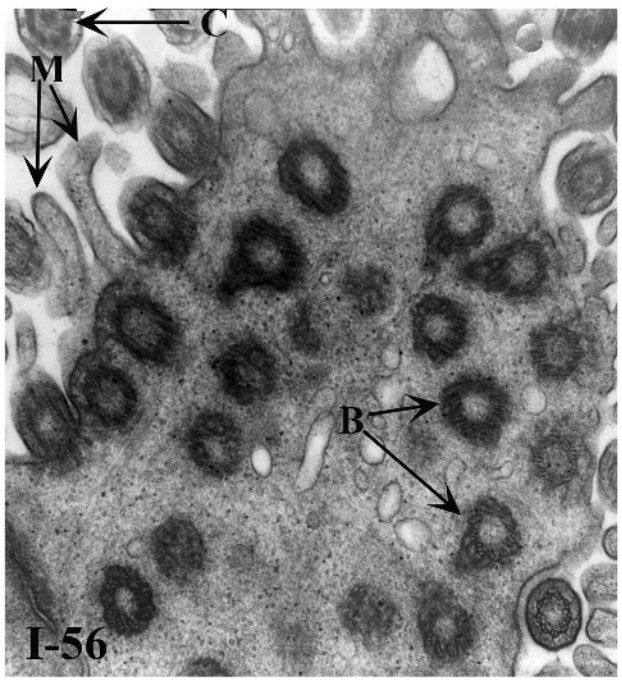
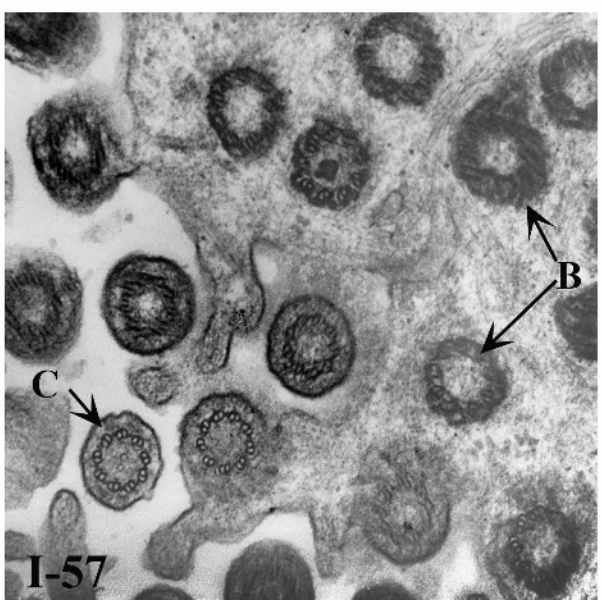
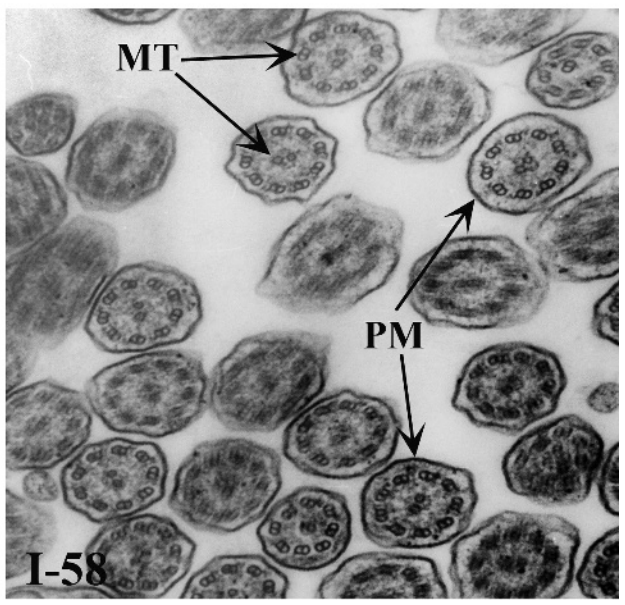


FIGURE I-54. Surface of lining epithelium of human trachea. ×4900. C, cilia.

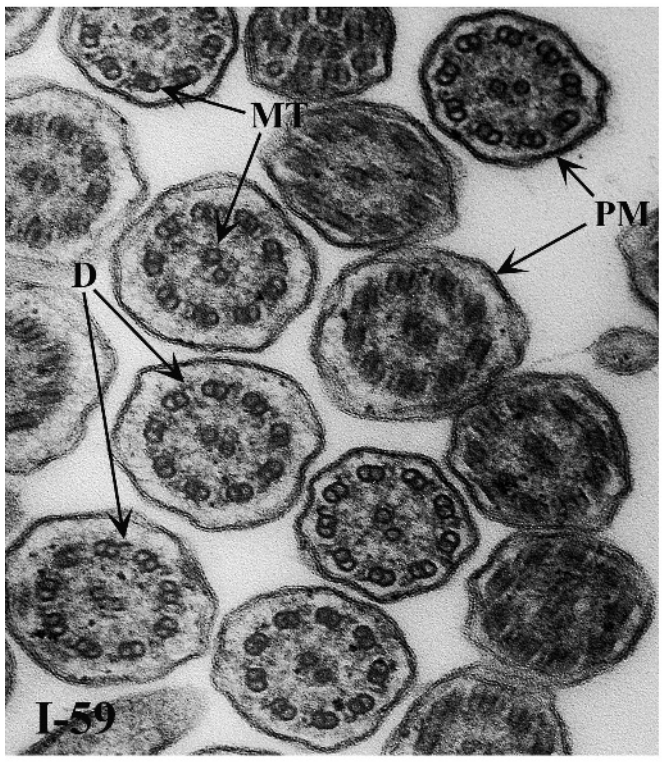


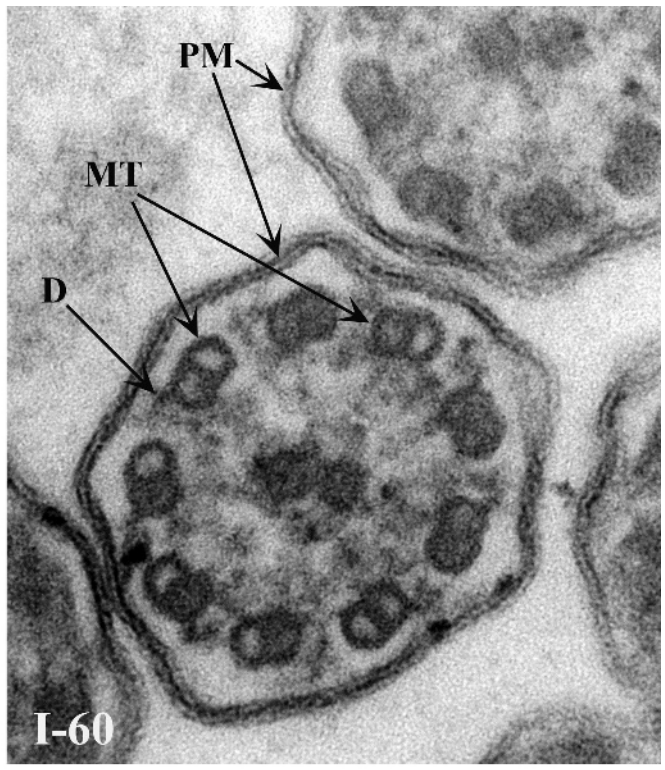


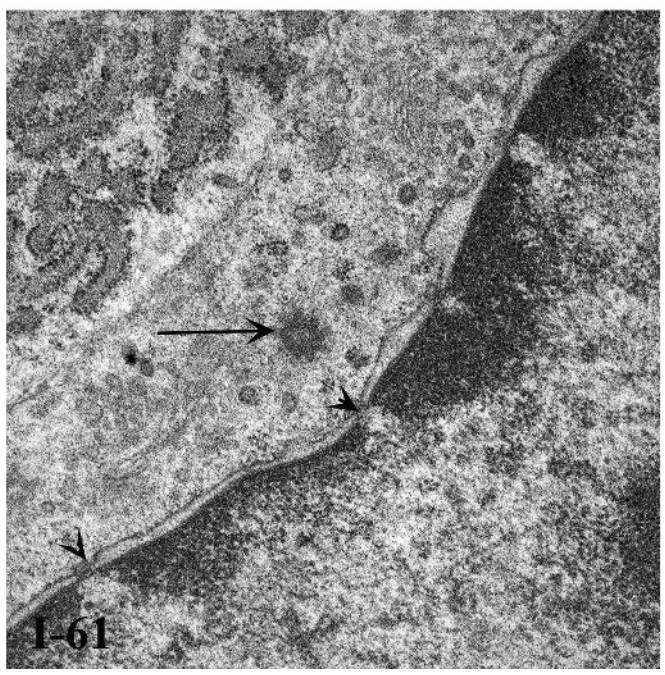


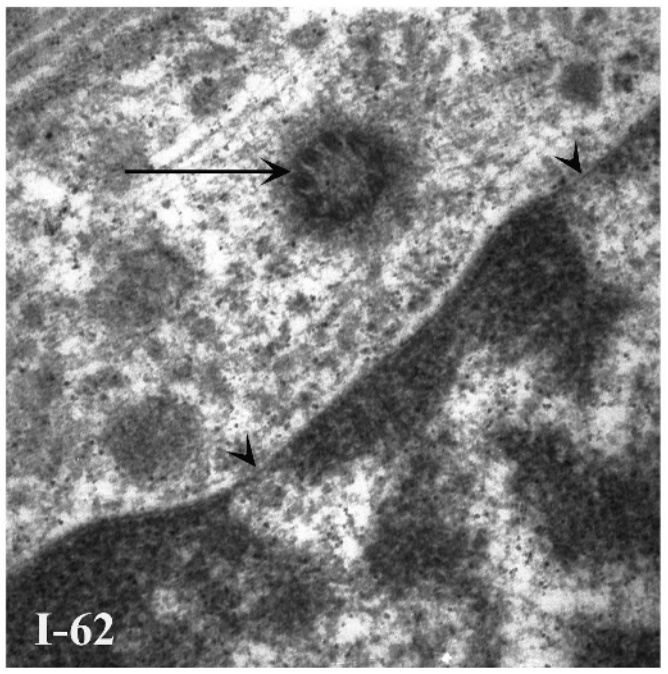


FIGURES I-55 to I-58. I-55 Apical border of bronchial epithelial cell showing microvilli and cilia. ×9032. I-56 Apical surface of bronchial epithelial cell showing microvilli (M), cilia (C), and basal portions of cilia (B). ×31 500. I-57 Apical surface of bronchial epithelial cell showing basal portions of cilia. ×46 095. I-58 Cross sections of cilia on the surface of bronchial epithelial cells showing axoneme cores. ×48 551. M, microvilli; B, basal portion of cilia; C, cilia; MT, microtubules of the axoneme core of cilia; PM, plasma membrane covering cilia.

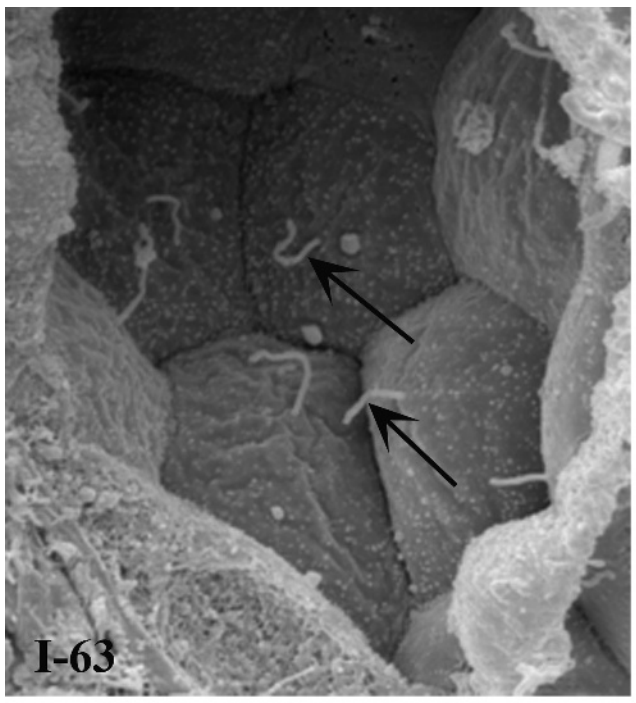


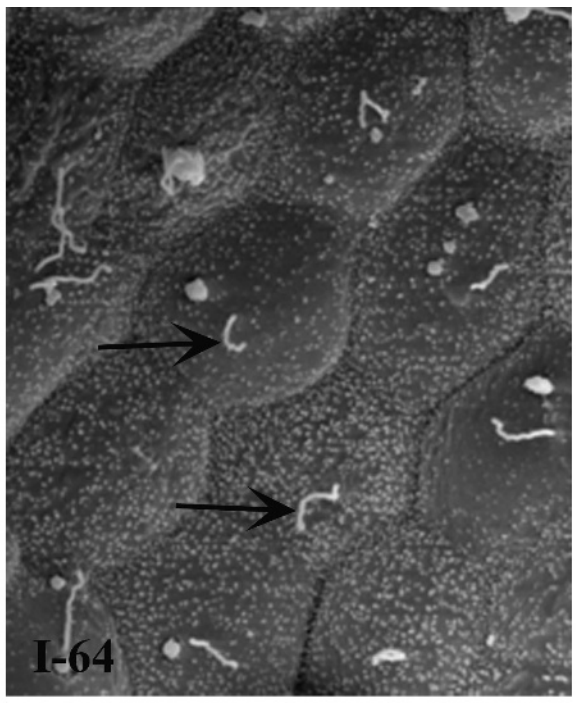


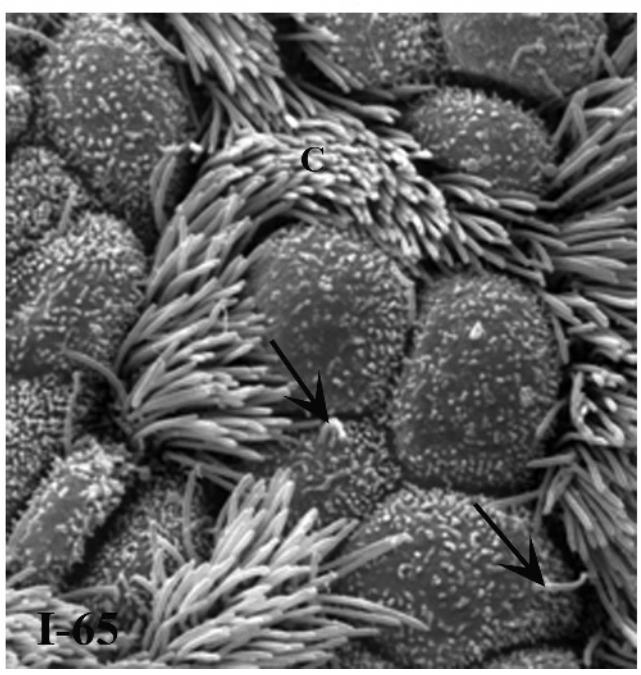




FIGURES I-59 to I-62. I-59 Cross sections of cilia from the human bronchus. Note "9 + 2" axoneme arrangement of microtubules in cores of cilia. ×89 760. I-60 Cross section of a single cilium from the human bronchus showing details of axoneme core ("9 + 2" arrangement of microtubules). ×247 500. I-61 Cell from human jejunum showing a centriole (arrow) and nuclear pores (arrowheads). ×80 000. I-62 High magnification of the edge of the nucleus of cell from human kidney showing a centriole (arrow) and nuclear pores (arrowheads). Note the ring of nine triplet microtubules making up the centriole. ×206 250. D, dynein side arms of microtubules; MT, microtubules; PM, plasma membranes.







Figures I-63 to I-65. I-63 Distal tubule in human kidney. Arrows, cilia. ×3200. I-64 Epithelial lining of Bowman's capsule in human kidney. Arrows, cilia. ×3200. I-65 Epithelial lining of ampulla segment of human oviduct. C, motile cilia; arrows, single central cilia. ×4400.

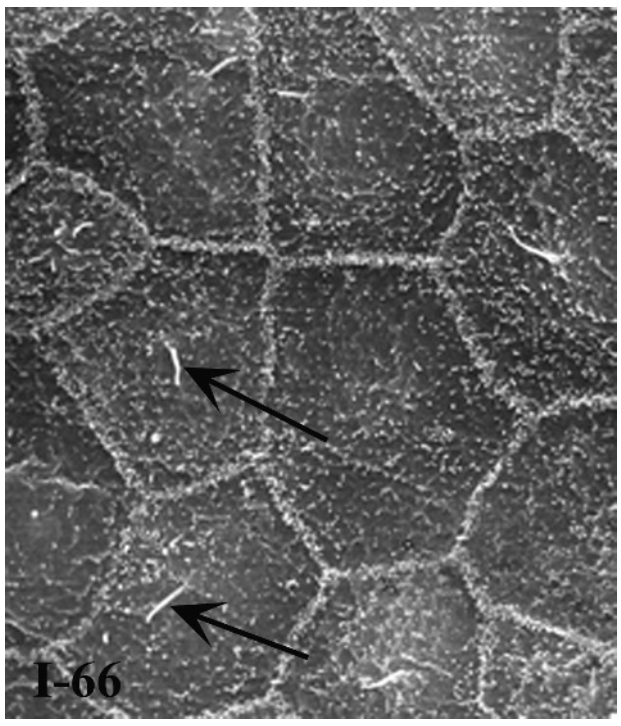
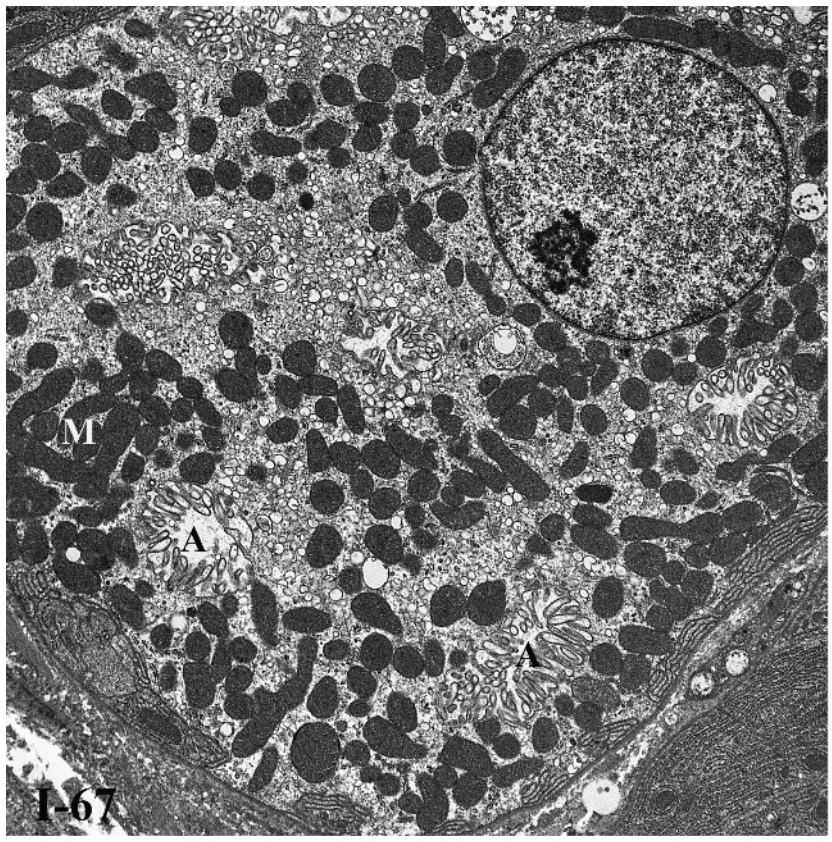
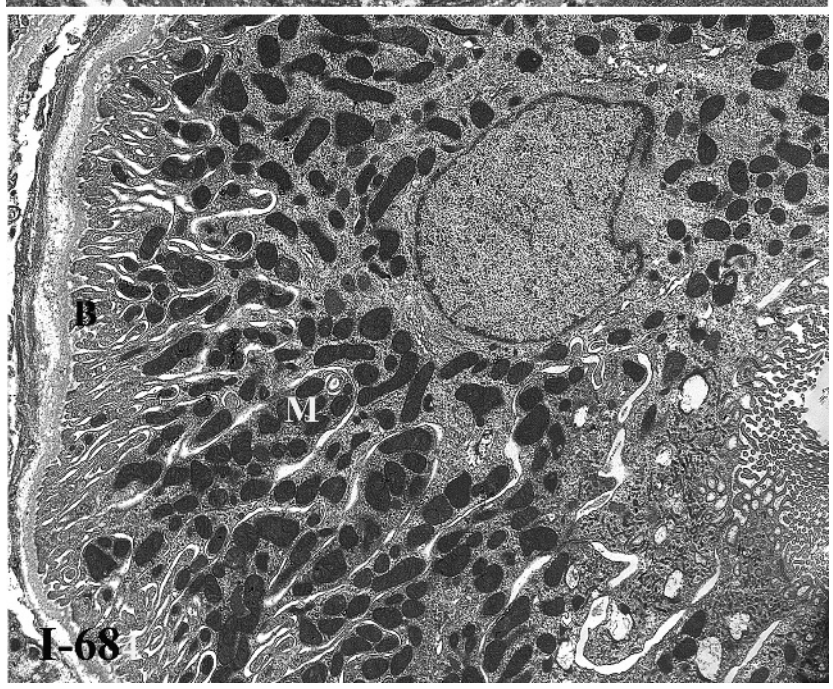


FIGURE I-66. Epithelial lining of follicle in human thyroid. ×3270. Arrows, single central cilia.

J. PLASMA MEMBRANE INFOLDINGS

In order to increase the surface area of cells for active transport or other purposes, the plasma membrane on the cell surface may be highly folded. This commonly occurs on either the baso-lateral surface or the apical surface of a cell. An example of a cell with extensive apical plasma membrane folds is the parietal cell located in a fundic gland of the stomach (Fig. I-67). This cell actively transports H^+ into the gastric lumen for HCl production. The hydrogen ion gradient between the parietal cell cytoplasm and the lumen of the stomach may be as high as 10^5 or 10^6 fold (neutral to very acidic pH), and thus the energy requirement for such transport is very high. An example of a cell with extensive baso-lateral plasma membrane folds is the proximal tubule cell in the kidney (Fig. I-68). This cell reabsorbs Na^+ from the glomerular filtrate, and then actively transports it through its baso-lateral cell membrane to the peritubular capillaries. Because of the need for ATP for active transport, the plasma membrane infoldings in these cells are often accompanied by high concentrations of mitochondria.





FIGURES I-67 to I-68. I-67 Parietal cell from human fundic stomach. Note that the multiple folds in the apical region (A) of plasma membrane are closely associated with many mitochondria (M). ×5714. I-68 Proximal tubule cell from human kidney. Note that the extensive folds in the baso-lateral plasma membrane (B) enclose many mitochondria (M). ×5306.