37

NUCLEUS AND ENDOPLASMIC RETICULUM

The nucleus of a cell contains virtually all of the hereditary material (DNA) that determines whether the cell will be a free-living single cell like an amoeba or will grow into a carrot, a rabbit, or some other kind of living thing. If the nucleus is removed by microsurgery, the cell will die. In contrast to the earlier plates on cells, which portrayed three-dimensional shapes, this plate shows the nucleus as it would appear in thin section under the electron microscope. Also shown is part of the endoplasmic reticulum, which is intimately associated with the nucleus.

Color the heading Nuclear Envelope and titles and structures A, B, and C. Choose a light color for C, and leave D uncolored. Retain your lightest colors for G and N.

D

The nucleus of eukaryotic cells is enclosed by two layers of membrane that are very similar to the cell membrane enclosing the entire cell. These two membranes comprise what is known as the nuclear envelope. At various points there are holes in this envelope called *nuclear pores,* created where the *outer membrane* turns in to join the *inner membrane.* These pores allow certain molecules manufactured in the nucleus to migrate out to the cytoplasm. The space between the inner and outer membranes of the nuclear envelope is called the *perinuclear space* (Greek: *peri,* "around"). The outer membrane is continuous with the endoplasmic reticulum at some points.

Color titles and structures E, F, and G. Use a very light color for G. Be aware that if the chromatin were drawn to scale, its diameter would be only about one-tenth of what is shown, and its total length would be several hundred thousand times what you are coloring here.

If a cell is stained, much of the stain is absorbed by a tangle of threads called *chromatin* (Greek: *chromos,* "color") spread throughout the nucleus. When a cell is preparing to divide into two cells, these threads coil up tightly into compact structures called chromosomes (Plate 65), but for most of the cell's life the chromatin is spread through the nucleus as shown here. At various points the chromatin is attached to the inner membrane of the nuclear envelope. Chromatin is made up of DNA, protein, and a very small amount of RNA. The most prominent structure in the nucleus is the *nucleolus,* which is not separated from the rest of the nucleus by a membrane but consists of fibers and granules so densely packed that it is easily distinguished from the surrounding chromatin. It consists of some DNA and a great deal of protein and RNA. Experiments have demonstrated that the fibers and granules are steps in the manufacture of the subunits that make the ribosomes found in such large numbers in the cytoplasm. The fluid that fills the rest of the nucleus is called the *nuclear sap.*

Color the rest of the titles and structures on the plate (H through N). Choose light colors for J, J^1, and N.

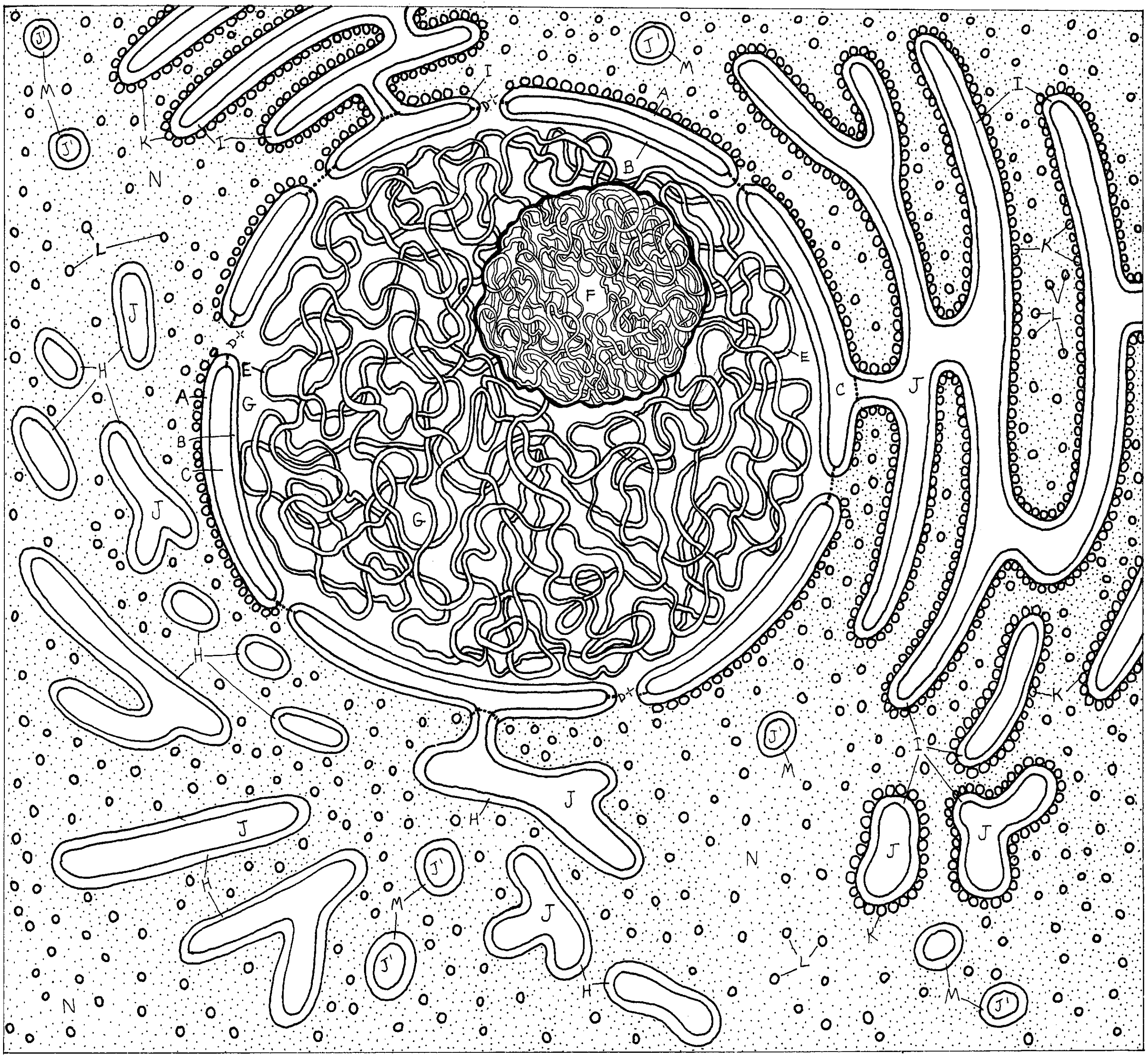
The endoplasmic reticulum (ER) is an extensive network of membranes within the cytoplasm. The membranes enclose numerous passageways called *cisternae* (singular, cisterna). Two different types of ER are distinguished by their overall appearance in electron micrographs: *rough ER,* which receives its rough appearance from the numerous ribosomes attached to it, and *smooth ER,* which has no ribosomes attached. The two types also differ in their structure and function. Rough ER tends to have much of its membrane arranged in flattened sheets, while most smooth ER is tubular, with many branches. (The three-dimensional views in Plate 30 show these features best. In this thin section, the tubes of the smooth ER are cut at various angles and don't look much like tubes.)

Rough ER serves to collect the proteins synthesized by the *attached ribosomes* and allow them to be transported within the cell. Most of those proteins are for export from the cell, and as they collect, the ER pinches off to form *vesicles* filled with protein. These vesicles then migrate either to the Golgi complex (see Plate 39) or to the cell membrane, where the proteins are released to the outside. *Free ribosomes* (not attached to the ER) synthesize proteins for use within the cell. The smooth ER synthesizes steroids and, in the liver, breaks down toxins and converts glycogen to glucose to maintain the proper level in the blood. In muscle, the smooth ER is more flattened and stores calcium ion, which it releases to produce muscular contraction. The fluid filling the rest of the space in the cytoplasm is called the *hyaloplasm.*

NUCLEUS AND ENDOPLASMIC RETICULUM.

NUCLEAR ENVELOPE ★
  OUTER MEMBRANE A
  INNER MEMBRANE B
  PERINUCLEAR SPACE C
  NUCLEAR PORE D✣
CHROMATIN E
NUCLEOLUS F
NUCLEAR SAP G
SMOOTH ENDOPLASMIC RETICULUM H

ROUGH ENDOPLASMIC RETICULUM I
CISTERNA J
ATTACHED RIBOSOME K
FREE RIBOSOME L
VESICLE M
  CONTENTS J'
HYALOPLASM N



38
MITOCHONDRION AND CHLOROPLAST

The mitochondrion (plural, mitochondria) is the organelle that combines oxygen with food molecules to obtain energy for the cell. Mitochondria are so tiny that they are difficult to see with the light microscope, even with special staining, but they are very visible with the electron microscope. They take a wide variety of shapes—including ovoid, spherical, branching, pear-shaped, and threadlike—and in the living cell actually change shape constantly. The number of mitochondria in any given cell depends on the metabolic activity of that cell. One known kind of cell has only one mitochondrion; liver cells, which are very active, usually have more than 1000; and a few cells are known to have more than 100,000.

Saving green for the chloroplasts, color title A and the mitochondria in the plant cell at the upper right of the plate. Then color titles and structures B through E. Choose a light color for E.

A *mitochondrion* has a smooth *outer membrane* and a greatly folded *inner membrane,* separated by a distinct *intermembrane space.* The inner membrane sends many projections called cristae (singular, crista) into the interior of the mitochondrion. Some of these are tubular, like the fingers of a glove, while others are sheetlike folds. The inner compartment of the mitochondrion is filled with a viscous fluid called the *matrix,* which is about half water and half protein.

The mitochondrion is the only place in the cell where oxygen can be combined with food molecules to release the energy in them for use by the cell. Although some energy can be released without the involvement of oxygen, it amounts to less than 10 percent in most cases. To get an idea of the value of mitochondria, suppose your average light lunch consists of a sandwich, an apple, a cupcake, and a soft drink. Without mitochondria, a light lunch would have to include at least ten sandwiches, ten apples, ten cupcakes, and ten soft drinks. You would also have to have a digestive tract ten times as large as your present one.

Color titles and structures F and G.

Mitochondria, along with chloroplasts, are unusual among organelles in containing some *DNA,* the molecule that carries the hereditary code, as well as their own *ribosomes* and the RNA molecules necessary to make their own proteins. Although they are dependent on the rest of the cell for some of their proteins, it is clear that they make many of their own. Both mitochondria and chloroplasts reproduce themselves as the cell grows without waiting for the cell to divide. This has led to the speculation that perhaps they were originally free-living prokaryotic cells that somehow became engulfed by eukaryotic cells and established a mutually beneficial relationship. They are, after all, about the size of prokaryotic cells, and their ribosomes are the same size and are composed of the same subunits as those of prokaryotic cells, which have ribosomes distinctly different from the ribosomes of eukaryotic cells.

Color title H green and color the chloroplasts (H) in the small plant cell at the upper right of the plate. Use a shade of green for title L as well, since the thylakoids (L) contain the chlorophyll responsible for making chloroplasts look green. Then color all the remaining titles and structures, including the heading Granum. Choose a pale color for Q.

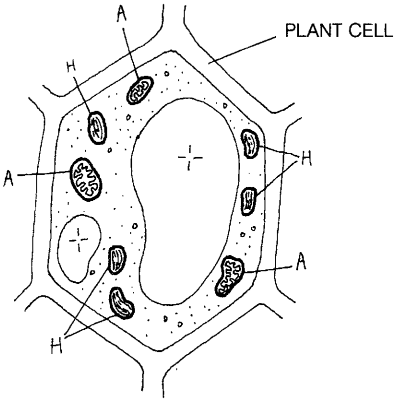
Although *chloroplasts* are found only in plants and algae, they are of immense importance to all living things, since virtually all of the energy used by living organisms in their life processes originally came from the sun and was trapped and converted to chemical energy by chloroplasts in the process of photosynthesis.

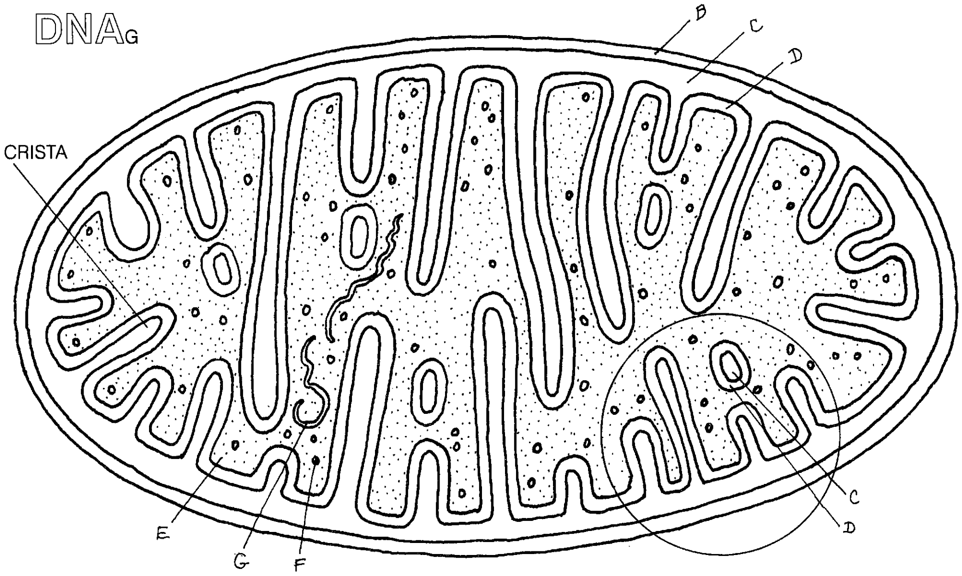
Like the mitochondrion, the chloroplast is surrounded by two *membranes.* Chlorophyll, the molecule that actually traps light energy, is found in flattened sacs called *thylakoids.* These thylakoids are arranged in stacks called grana (singular, granum), and some of them are connected to others by extensions called *stromal lamellae* (singular, lamella). The semifluid material that fills all the remaining space in the chloroplast is called the *stroma.* As mentioned, chloroplasts contain *DNA* and *ribosomes* and reproduce independently of the cell.

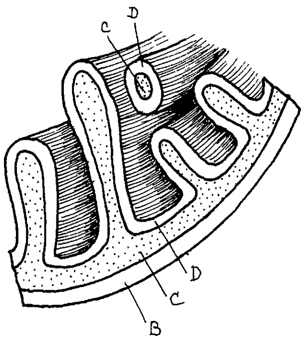
The principal product of photosynthesis is glucose, some of which is assembled into starch molecules and collected into *starch grains* within the chloroplast.

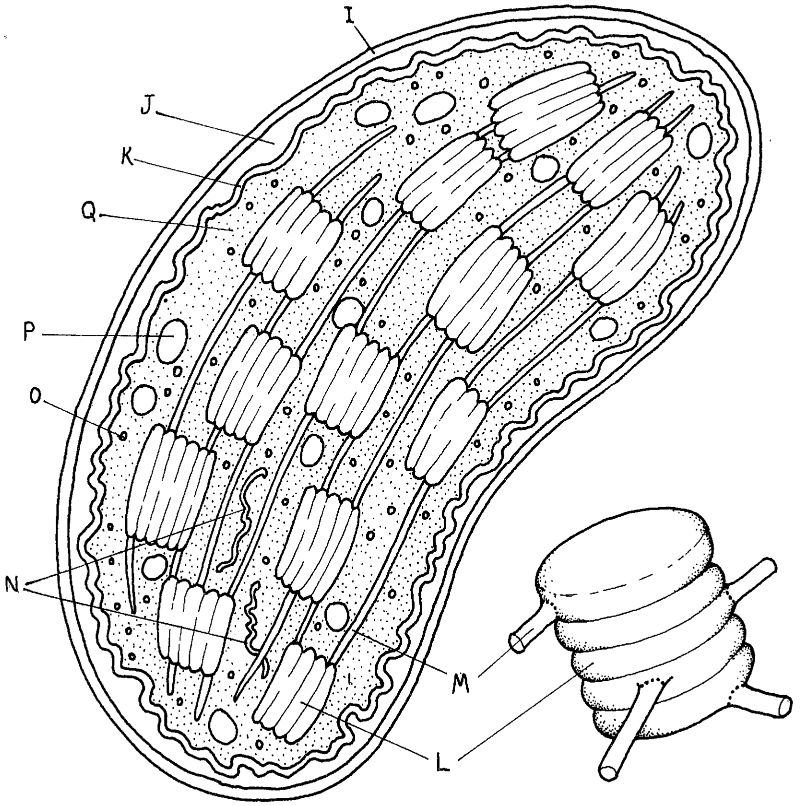
MITOCHONDRION AND CHLOROPLAST.

MITOCHONDRION$_A$
OUTER MEMBRANE$_B$
INTERMEMBRANE SPACE$_C$
INNER MEMBRANE$_D$
MATRIX$_E$
RIBOSOME$_F$
DNA$_G$









CHLOROPLAST$_H$
OUTER MEMBRANE$_I$
INTERMEMBRANE SPACE$_J$
INNER MEMBRANE$_K$
GRANUM$_\star$
THYLAKOID$_L$
STROMAL LAMELLA$_M$
DNA$_N$
RIBOSOME$_O$
STARCH GRAIN$_P$
STROMA$_Q$

39

GOLGI COMPLEX, LYSOSOMES, MICROBODIES

The Golgi complex was discovered in the late nineteenth century by Camillo Golgi, who used a complex silver stain that didn't always work. This led some scientists to question its existence. However, the modern electron microscope has disclosed that the Golgi complex really is a distinctive organelle, present in all eukaryotic cells.

Color the headings Golgi Complex and Saccule/ Vesicle and titles and structures A through B^1 at the upper right. Choose a pale color for B and B^1.

A Golgi complex consists of a stack of flattened membranous sacs, called saccules, and a number of tiny sacs called vesicles, which are budded off from the saccules at their edges. An animal cell will generally have between 10 and 20 Golgi complexes; a plant cell will usually have many more than that, sometimes as many as 200, although they are much smaller. These small Golgi complexes in plants are usually called dictyosomes.

Color the heading Golgi Complex in Action and titles and structures C through I of the animal cell at the bottom of the plate.

The function of the Golgi complex is to assemble simple molecules into complex ones and package them for use elsewhere. Complex carbohydrates are made there, and the assembly of complex proteins is completed. The *amino acids* making up complex proteins are first assembled into *polypeptide chains* (see Plate 18) by *ribosomes* attached to the *rough endoplasmic reticulum.* The polypeptides pass into the *cisternae* of the rough ER as they are being made. Sometimes glucose and a few other sugars are added to the polypeptides while they are in the cisternae. They then move to the *smooth ER,* where they are pinched off into vesicles at the end of a *cisterna,* becoming enclosed in a small piece of ER membrane. The resulting vesicle is called a *transition vesicle* because the polypeptide molecules are in transition from the ER to the Golgi complex.

Color the Golgi saccules (A and B + G) and titles and structures J and K.

When the transition vesicle reaches the Golgi complex, the vesicle membrane fuses with the *Golgi membrane,* emptying the polypeptides into the *Golgi saccule compartment.* There the polypeptides have numerous sugars, lipids, or other molecules attached to them. The completed *protein complexes* then migrate to the end of the Golgi saccule and are pinched off within a piece of membrane to form a Golgi vesicle. If that particular protein is for "export" (secretion), the Golgi saccule, called a *secretion vesicle,* migrates to the surface of the cell, where it will fuse with the *cell membrane,* emptying its contents to the exterior in a process called exocytosis (the reverse of endocytosis, explained in Plate 33).

Color the remaining parts of the plate.

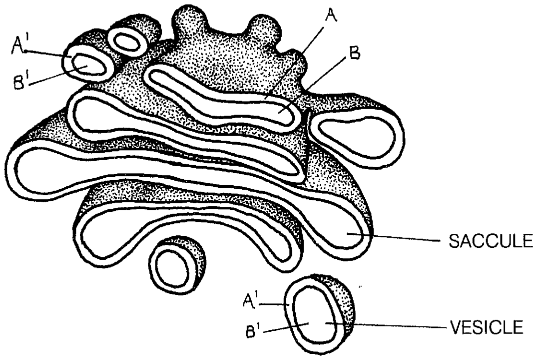
The ER and the Golgi complex also cooperate to manufacture many enzymes (which are also *protein complexes*). Enzymes are capable of hydrolyzing ("breaking down"; see Plate 16) all kinds of large molecules. These are also pinched off into vesicles, but such vesicles are called *lysosomes* (Greek: *lysis,* "loosening" or "breaking"; *soma,* "body") because the enzymes they contain cause complex molecules to come apart into their components. It is not known how the lysosome membrane avoids being itself hydrolyzed by the enzymes, but if lysosomes are broken open, they may digest the entire cell. This occurrence is a normal part of the development of an embryo, as when a human embryo reabsorbs the tail (that is present in the early stages) and the webs between the fingers and toes.

In cells that take in materials by endocytosis, lysosomes fuse with the *food vacuole,* emptying their enzymes into the vacuole to digest the *food.* Lysosomes also engulf and break down worn-out cell organelles. It is not uncommon to find lysosomes with parts of mitochondria inside them being digested. Lysosomes are absent from the cells of most plants. Instead, the same hydrolytic enzymes are found in the central vacuole or occasionally in certain plastids.

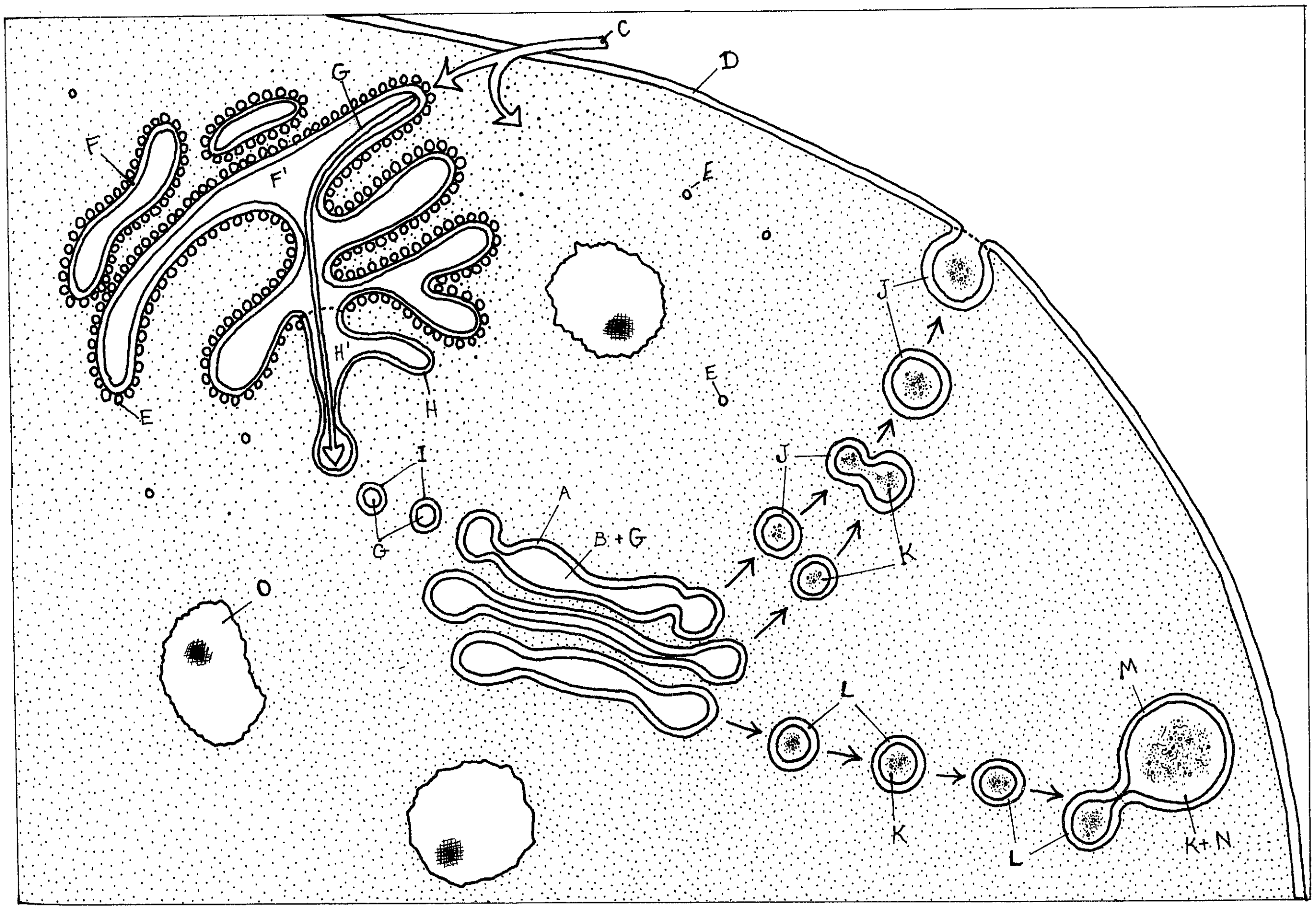
Cells have been found to contain other kinds of membrane-enclosed vesicles very similar to lysosomes. These were originally called microbodies, but it is now clear that there are at least two types. They, too, contain enzymes, but for different purposes. *Peroxisomes* contain enzymes that break down hydrogen peroxide. Hydrogen peroxide is a by-product of the breakdown of amino acids and uric acid by other enzymes present in the peroxisome. A regular, crystalline structure, presumed to be a crystal of enzymes, is often seen in the center. Glyoxysomes (not shown) have been found only in plants. They contain enzymes that extract energy from glucose in a series of chemical reactions known as the glyoxylate cycle.

GOLGI COMPLEX, LYSOSOMES, MICROBODIES.

GOLGI COMPLEX★
SACCULE/VESICLE★
  MEMBRANE$_{A,A^1}$
  COMPARTMENT$_{B,B^1}$
GOLGI COMPLEX IN ACTION★
AMINO ACID MOLECULES$_C$
CELL MEMBRANE$_D$
RIBOSOME$_E$
ROUGH ER MEMBRANE$_F$
  CISTERNA$_{F^1}$
POLYPEPTIDE CHAINS$_G$
SMOOTH ER MEMBRANE$_H$
  CISTERNA$_{H^1}$
TRANSITION VESICLE$_I$



SECRETION VESICLE$_J$
  PROTEIN COMPLEX$_K$
LYSOSOME$_L$
FOOD VACUOLE$_M$
  FOOD$_N$
MICROBODY★
  PEROXISOME$_O$



40

MICROFILAMENTS AND MICROTUBULES

Microfilaments and microtubules are responsible for maintaining cell shape and for virtually all movement in eukaryotic cells. The more common kinds of microfilaments are only 5 to 7 nanometers in diameter, and microtubules are only 20 to 25 nanometers in diameter. Although there is still considerable uncertainty, movement seems to result from numerous projections that reach out from one microfilament to another or from one microtubule to another and then shorten, pulling the microfilaments or microtubules past one another, much as the crew of a sailboat will pull in the anchor by standing in a line and pulling in the anchor rope hand over hand. The proteins comprising microfilaments are, however, entirely different from those comprising microtubules, and the two apparently never interact.

Color the headings Relaxed Sarcomere and Contracted Sarcomere and titles and structures A through E. Use a light color for A.

The microfilaments that have been most extensively studied are those found in the *skeletal muscle* of animals with backbones. This type of muscle is also called striated muscle because of the striations (stripes) that divide it into the light and dark bands illustrated in the upper right drawing. The striations result from alternating areas of overlap of thick and thin microfilaments. Each skeletal muscle cell is divided into numerous contractile units called sarcomeres, 1.5 to 2.5 nanometers long, depending on the state of contraction or relaxation. Each sarcomere is separated from the next by a partition called the *Z-line* (or Z-disk). Extending toward the center of the sarcomere from the Z-line at each end are numerous *thin microfilaments* of a protein called actin, with smaller amounts of two other proteins, troponin and tropomyosin, attached. Between the thin microfilaments are *thick microfilaments* that extend from the center of the sarcomere toward the Z-lines. The thick microfilaments are composed of a protein known as myosin and have numerous projections, which are commonly called *cross-bridges,* since they appear to cross over and attach to the thin microfilaments. The current "sliding filament theory" of muscular contraction is based on the belief that the cross-bridges attach to the thin microfilaments and pull them past the thick microfilaments so that the sarcomere shortens. Notice that in the contracted sarcomere, cross-bridges have attached to the thin microfilaments.

When the sarcomere is fully shortened, the thin microfilaments overlap somewhat in the center, and the Z-lines are drawn in until they almost touch the ends of the thick microfilaments. If enough sarcomeres shorten, the entire muscle shortens.

Color the heading Ratchet Action, titles F and G, and the associated illustration.

The movement of the cross-bridges is often compared to the action of a ratchet. Each cross-bridge apparently reaches out and attaches to a thin microfilament at an angle of 90 degrees, then moves (in the power stroke) to an angle of 45 degrees, forcing the thin microfilament to move a short distance; then it detaches to return (in the recovery stroke) to the 90-degree position for a new attachment. With numerous cross-bridges going through this same process, the microfilaments are made to slide past one another, and the sarcomere shortens.

Color the heading Cytoskeleton/Cytomusculature and titles H and I. Color over the fine lines representing the microfilaments and the microtubules.

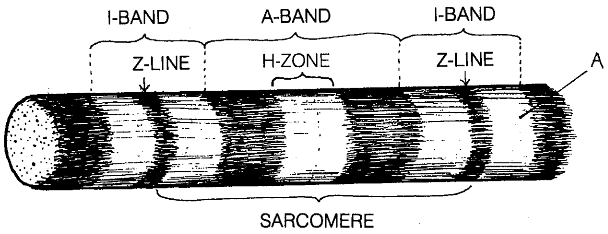
Microfilaments are found in most cells, but in much less organized patterns than in muscle cells. In some cases they seem merely to provide a support to hold the cell in a particular shape and have come to be regarded as a sort of cytoskeleton ("cell skeleton"). In other cases they seem to be involved in the movement of the cell or of parts within the cell and are referred to as cytomusculature ("cell muscle system"). They are composed mostly of actin, but myosin is often present, particularly where movement is involved. *Microtubules* are generally more rigid than microfilaments and appear to have a larger role in determining cell shape, but they are also responsible for certain kinds of movement within the cell.

Color titles and structures J and K.

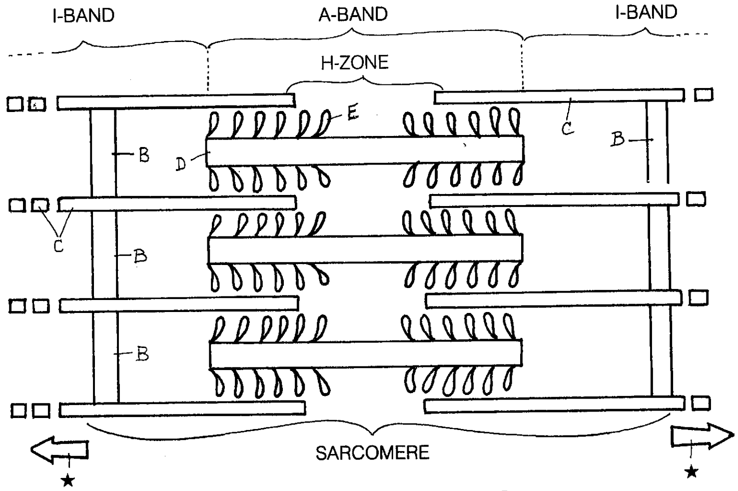
Microtubules do not consist of the same proteins found in microfilaments. Instead they are made up of two other proteins, *α-tubulin* and *β-tubulin.* These are assembled into dimers (double molecules), which in turn become assembled into left-handed spirals. In this form they are useful as structural elements for the cell; with other proteins attached, they can also produce movement, as you will see in the next plate.

MICROFILAMENTS AND MICROTUBULES.

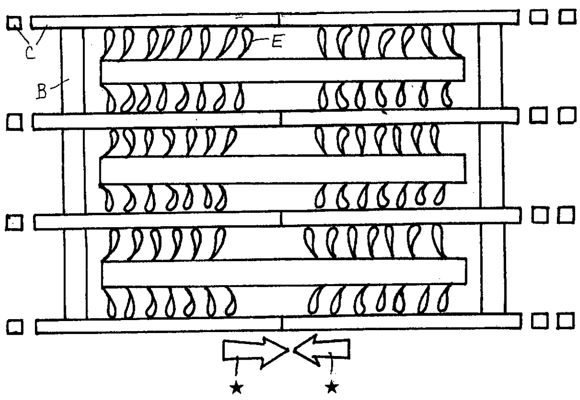
SKELETAL MUSCLE CELL$_{A}$
Z-LINE$_{B}$
THIN MICROFILAMENT$_{C}$
THICK MICROFILAMENT$_{D}$
CROSS-BRIDGE$_{E}$



RELAXED SARCOMERE★

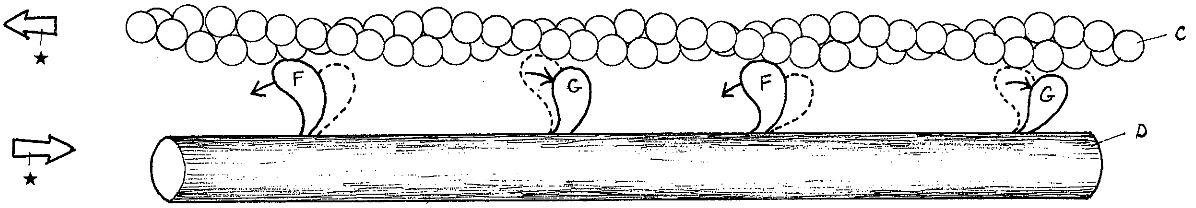


CONTRACTED SARCOMERE★



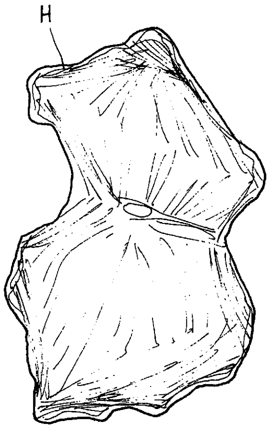
RATCHET ACTION★

CROSS-BRIDGE IN POWER STROKE$_{F}$
CROSS-BRIDGE IN RECOVERY STROKE$_{G}$

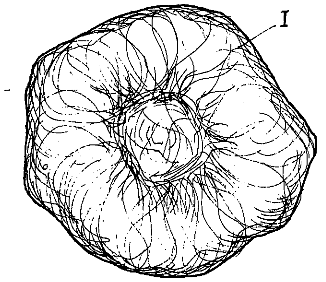


CYTOSKELETON/CYTOMUSCULATURE★

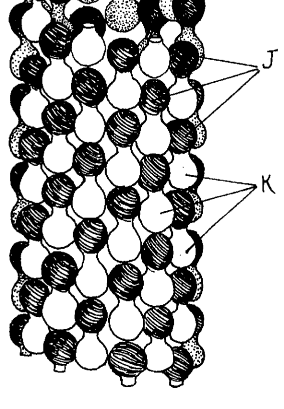
MICROFILAMENTS$_{H}$



MICROTUBULES$_{I}$



α-TUBULIN$_{J}$
β-TUBULIN$_{K}$



41
CILIA AND FLAGELLA

The earliest discoveries with the microscope included some single-celled creatures that propel themselves by cilia or flagella (Latin: *cilium,* "eyelash"; *flagellum,* "whip").

Color titles and illustrations A and B with pale colors.

Paramecium has about 2000 cilia on its single cell. Cilia are also used for locomotion in small multicellular animals and in large ones for movement of materials in tubes of the reproductive and respiratory tracts. Whereas cilia are short and numerous, flagella are long and usually single, as in *Euglena* or in the male reproductive cell (sperm cell) of a multicellular animal. Some algae cells have two or more flagella.

For all the differences apparent in the light microscope, however, cilia and flagella appear to be identical when observed with the electron microscope, except for the obvious difference in length.

Color the headings Microtubules and Doublet and titles C through K. Color each part of the large cilium on the left side of the plate as it is discussed in the text. Use contrasting colors for C and D and a very bright color for J.

In the electron microscope it becomes clear that cilia and flagella are composed of microtubules arranged in the same precise pattern. In the movable portion, which extends beyond the body of the cell, there are nine microtubule doublets around the perimeter. Each doublet consists of two subtubules, an *A subtubule* (slightly closer to the center) and an attached *B subtubule.* In the center are two single microtubules, commonly called *singlets.* (This pattern is commonly called the "9 + 2" configuration.) The base of the cilium or flagellum (known as the basal body), which anchors it within the cell, has a "9 + 0" configuration: nine microtubule triplets around the perimeter and no central singlets. Each triplet consists of an A subtubule (distinctly closer to the center) and attached B and *C subtubules.* The C subtubules do not extend past the body of the cell, but the A and B subtubules are continuous from the basal body to the tip of the cilium or flagellum.

Detailed studies with the electron microscope have disclosed filaments called *spokes* that join each A subtubule to *sheath elements* surrounding the central singlets at regular intervals. In addition, filaments of a protein called *nexin* join each A subtubule to the B subtubule of the next doublet. Each A subtubule also has two projecting arms of a protein called *dynein,* which is believed to produce the movement by reaching up or down to attach to the B subtubule of the next doublet at a different level and then pulling the tubules past one another in a manner similar to the sliding of microfilaments in muscle.

Color the heading Mechanism of Bending and the related illustrations.

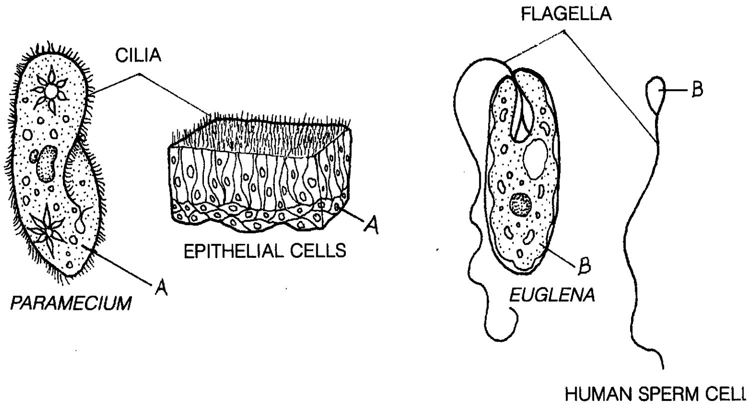
This section shows how a cilium or flagellum is made to bend. Suppose that a cilium is to bend to the right. The dynein arms of the doublets on the right side of the cilium reach up and attach to the adjacent doublets at a higher level. At the same time, the dynein arms of the doublets on the left side (not shown) reach down and attach at a lower level. Then the dynein arms contract, causing the doublets on the right to move up relative to the doublets on the left. Since the doublets are anchored in the basal body, the only way they can move relative to one another is to force the cilium to bend to the right.

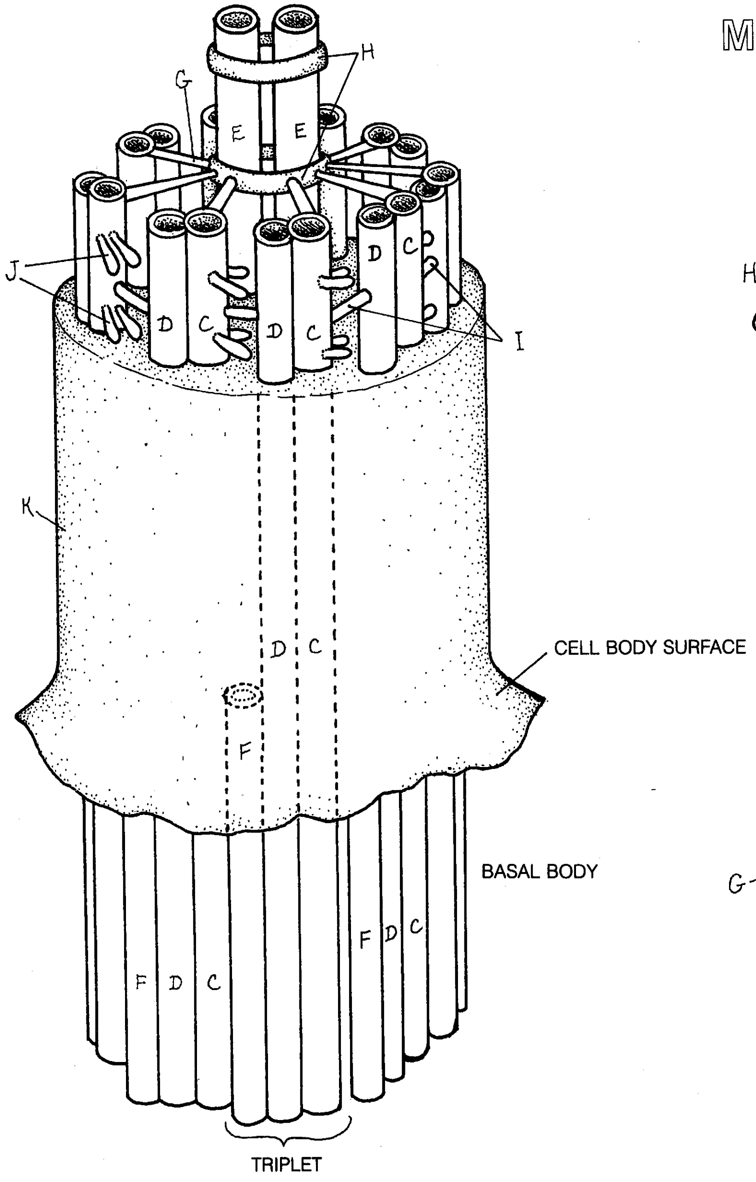
The "9 + 0" pattern of the basal body is also exactly what we find in centrioles, which were discussed in Plate 30 and will come up again when we discuss cell division in animals (Plate 65). Originally it was a great mystery why these two different organelles should have identical structures. Today we know that when a cell needs to produce more cilia or flagella, the centrioles reproduce themselves, and the "daughter" centrioles migrate to the cell membrane and become basal bodies, extending the A and B subtubules of each triplet to push the cell membrane out and form the rest of the cilium or flagellum.

CILIA AND FLAGELLA.

MICROTUBULES★
DOUBLET★
SUBTUBULE A$_C$
SUBTUBULE B$_D$
SINGLET$_E$
SUBTUBULE C$_F$
SPOKE$_G$
SHEATH ELEMENT$_H$
NEXIN$_I$
DYNEIN$_J$
CELL MEMBRANE$_K$

CELLS WITH CILIA$_A$
CELLS WITH A FLAGELLUM$_B$





MECHANISM OF BENDING★