Chapter 7

Membrane Structure and Function

Key Concepts

7.1 Cellular membranes are fluid mosaics of lipids and proteins

7.2 Membrane structure results in selective permeability

7.3 Passive transport is diffusion of a substance across a membrane with no energy investment

7.4 Active transport uses energy to move solutes against their gradients

7.5 Bulk transport across the plasma membrane occurs by exocytosis and endocytosis

Framework

This chapter presents the fluid mosaic model of membrane structure, relating the molecular structure of biological membranes to their function of regulating the passage of substances into and out of the cell.

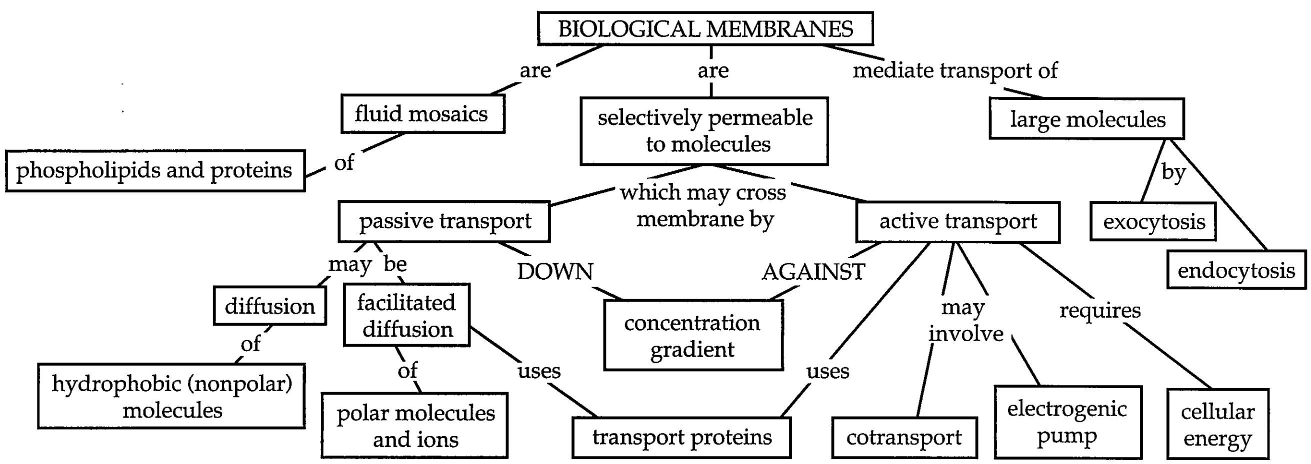
Chapter Review

The plasma membrane is the boundary of life; this **selectively permeable** membrane allows the cell to maintain a unique internal environment and to control the movement of materials into and out of the cell.

7.1 Cellular membranes are fluid mosaics of lipids and proteins

According to the currently accepted **fluid mosaic model,** the structure of biological membranes consists of various proteins that are attached to or embedded in a bilayer of **amphipathic** phospholipids.

Membrane Models: Scientific Inquiry Early chemical analysis of membranes revealed a lipid and protein composition. In 1925 two Dutch scientists suggested that cell membranes must be a phospholipid bilayer, with the hydrophobic hydrocarbon tails in the center and the hydrophilic heads facing the aqueous solution on both sides of the membrane. In 1935 H. Davson and J. Danielli proposed a model in which a double layer of phospholipids is covered with a coat of hydrophilic proteins. This sandwich model was consistent with the first views of membranes seen with electron microscopy, and by the



1960s, the Davson-Danielli model was widely accepted for all cellular membranes.

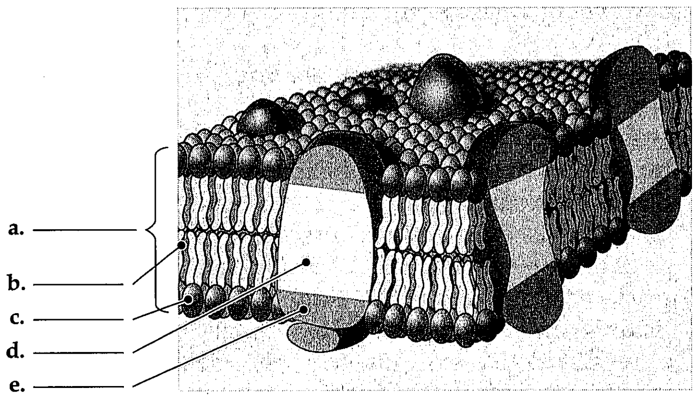
In 1972 S. J. Singer and G. Nicolson proposed their fluid mosaic model in which amphipathic membrane proteins are embedded in the phospholipid bilayer with their hydrophilic regions extending out into the aqueous environment. The phospholipid bilayer is envisioned as fluid, with a mosaic of protein molecules floating in it.

The fluid mosaic model is supported by evidence from freeze-fracture electron microscopy. This technique involves freezing a specimen, fracturing it with a cold knife, and examining the exposed interior of a membrane with the electron microscope.

The fluid mosaic model is currently the most accepted and useful model for organizing existing knowledge and extending further research on membrane structure.

■ INTERACTIVE QUESTION 7.1

Label the components in this diagram of the fluid mosaic model of membrane structure. Indicate the regions that are hydrophobic and those that are hydrophilic.



The Fluidity of Membranes Membranes are held together primarily by weak hydrophobic interactions that allow the lipids and some of the proteins to drift laterally. Some membrane proteins seem to be held rigid by attachments to the cytoskeleton; others appear to be directed in their movements by cytoskeletal fibers.

Phospholipids with unsaturated hydrocarbon tails maintain membrane fluidity at lower temperatures. The steroid cholesterol, common in plasma membranes of animals, restricts movement of phospholipids and thus reduces fluidity at warmer temperatures. Cholesterol also prevents the close packing of lipids and thus enhances fluidity at lower temperatures.

■ INTERACTIVE QUESTION 7.2

a. Cite some experimental evidence that shows that membrane proteins drift.

b. How might the plasma membrane of a plant cell change in response to the cold temperatures of winter?

Membrane Proteins and Their Functions Each membrane has its own unique complement of membrane proteins, which determine most of the specific functions of that membrane. **Integral proteins** often extend through the membrane (transmembrane), with two hydrophilic ends and a hydrophobic midsection, usually consisting of one or more α-helical stretches of hydrophobic amino acids. **Peripheral proteins** are attached to the surface of the membrane, often to integral proteins. Attachments of membrane proteins to the cytoskeleton on the cytoplasmic side and fibers of the extracellular matrix on the exterior provide a supportive framework for the plasma membrane.

■ INTERACTIVE QUESTION 7.3

List the six major kinds of functions that membrane proteins may perform.

The Role of Membrane Carbohydrates in Cell-Cell Recognition The ability of a cell to distinguish other cells is based on recognition of membrane carbohydrates. The **glycolipids** and **glycoproteins** attached to the outside of plasma membranes vary from species to species, from individual to individual, and even among cell types.

Synthesis and Sidedness of Membranes Membranes have distinct inner and outer faces, related to the composition of the lipid layers, the directional orientation of their proteins, and the attachment of carbohydrates to the exterior surface. Carbohydrates are attached to membrane proteins as they are synthesized in the ER and modified in the Golgi, and attached to lipids in the Golgi. When transport vesicles fuse with the plasma membrane, these interior glycoproteins and glycolipids become located on the exterior face of the membrane.

7.2 Membrane structure results in selective permeability

The plasma membrane permits a regular exchange of nutrients, waste products, oxygen, and inorganic ions. Biological membranes are selectively permeable; the ease and rate at which small molecules pass through them differ.

The Permeability of the Lipid Bilayer Hydrophobic, nonpolar molecules, such as hydrocarbons, CO_2, and O_2, can dissolve in and cross through a membrane.

■ INTERACTIVE QUESTION 7.4

What types of molecules have difficulty crossing the plasma membrane? Why?

Transport Proteins Ions and polar molecules may move across the plasma membrane with the aid of **transport proteins.** Hydrophilic passageways through a membrane are provided for specific molecules by channel proteins, such as **aquaporins,** which facilitate water passage. Carrier proteins may physically bind and transport a specific molecule.

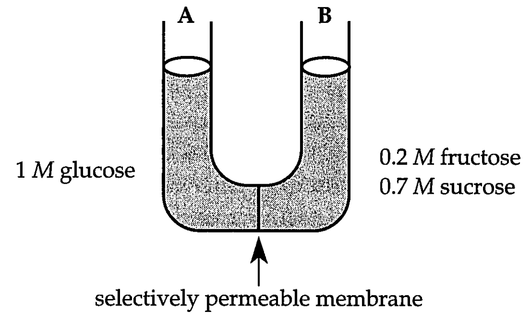
7.3 Passive transport is diffusion of a substance across a membrane with no energy investment

Diffusion **Diffusion** is the movement of a substance down its **concentration gradient** due to random thermal motion. The diffusion of one solute is unaffected by the concentration gradients of other solutes. The cell does not expend energy when substances diffuse across membranes down their concentration gradient; therefore, the process is called **passive transport.**

Effects of Osmosis on Water Balance **Osmosis** is the diffusion of water across a selectively permeable membrane. Water diffuses down its own concentration gradient, which is affected by the solute concentration. Binding of water molecules to solute particles lowers the proportion of unbound water that is free to cross the membrane.

■ INTERACTIVE QUESTION 7.5

A solution of 1 *M* glucose is separated by a selectively permeable membrane from a solution of 0.2 *M* fructose and 0.7 *M* sucrose. The membrane is not permeable to the sugar molecules. Indicate which side initially has more free water molecules and which has fewer. Show the direction of osmosis.



Tonicity, the tendency of a cell to gain or lose water in a given solution, is affected by the permeability of the plasma membrane and whether or not the cell has a wall. An animal cell will neither gain nor lose water in an **isotonic** environment. An animal cell placed in a **hypertonic** environment will lose water and shrivel. If placed in a **hypotonic** solution, the cell will gain water, swell, and possibly lyse (burst). Cells without rigid walls must either live in an isotonic environment, such as salt water or isotonic body fluids, or have adaptations for **osmoregulation,** the control of water balance.

■ INTERACTIVE QUESTION 7.6

a. What osmotic problems do freshwater protists face?

b. What adaptations may help them osmoregulate?

The cell walls of plants, fungi, prokaryotes, and some protists play a role in water balance within hypotonic environments. Water moving into the cell causes the cell to swell against its cell wall, creating a turgid cell. **Turgid** cells provide mechanical support for nonwoody plants. Plant cells in an isotonic surrounding are **flaccid.** In a hypertonic medium, a plant cell undergoes **plasmolysis,** the pulling away of the plasma membrane from the cell wall as water leaves and the cell shrivels.

■ **INTERACTIVE QUESTION 7.7**

a. The ideal osmotic environment for animal cells is __________.

b. The ideal osmotic environment for plant cells is __________.

Facilitated Diffusion: Passive Transport Aided by Proteins **Facilitated diffusion** involves the diffusion of polar molecules and ions across a membrane with the aid of transport proteins, either channel proteins or carrier proteins. Aquaporins greatly speed up diffusion of water. Many **ion channels** are **gated channels,** which open or close in response to electrical or chemical stimuli.

The binding of the solute to a carrier protein may cause a conformational change that serves to translocate the binding site and attached solute across the membrane.

■ **INTERACTIVE QUESTION 7.8**

Why is facilitated diffusion considered passive transport?

7.4 Active transport uses energy to move solutes against their gradients

The Need for Energy in Active Transport **Active transport,** requiring the expenditure of energy by the cell, is essential for a cell to maintain internal concentrations of small molecules that differ from environmental concentrations. The terminal phosphate group of ATP may be transferred to a carrier protein, inducing it to change its conformation and translocate the bound solute across the membrane. The **sodium-potassium pump** works this way to exchange Na^+ and K^+ across animal cell membranes, creating a greater concentration of potassium ions and a lesser concentration of sodium ions within the cell.

Maintenance of Membrane Potential by Ion Pumps Cells have a **membrane potential,** a voltage across the plasma membrane due to the unequal distribution of ions. This electrical potential energy results from the separation of opposite charges: The cytoplasm of a cell is negatively charged compared to extracellular fluid. The membrane potential favors the diffusion of cations into the cell and anions out of the cell. Both the membrane potential and the concentration gradient affect the diffusion of an ion; thus, an ion diffuses down its **electrochemical gradient.**

Electrogenic pumps are membrane proteins that generate voltage across a membrane by the active transport of ions. **A proton pump** that transports H^+ out of the cell generates membrane potentials in plants, fungi, and bacteria.

■ **INTERACTIVE QUESTION 7.9**

The Na^+-K^+ pump, the major electrogenic pump in animal cells, exchanges sodium ions for potassium ions, both of which are cations. How does this exchange generate a membrane potential?

Cotransport: Coupled Transport by a Membrane Protein **Cotransport** is a mechanism through which the active transport of a solute is indirectly driven by an ATP-powered pump that transports another substance against its gradient. As that substance diffuses back down its concentration gradient through a specialized cotransporter, the solute is carried against its concentration gradient across the membrane.

7.5 Bulk transport across the plasma membrane occurs by exocytosis and endocytosis

Exocytosis In **exocytosis,** the cell secretes macromolecules by the fusion of vesicles with the plasma membrane.

Endocytosis In **endocytosis,** a region of the plasma membrane sinks inward and pinches off to form a vesicle containing material that had been outside the cell. **Phagocytosis** is a form of endocytosis in which pseudopodia wrap around a food particle, creating a vacuole that then fuses with a lysosome containing hydrolytic enzymes. In **pinocytosis,** droplets of extracellular fluid are taken into the cell in small vesicles. **Receptor-mediated endocytosis** allows a cell to acquire specific substances from extracellular fluid. **Ligands,** molecules that bind specifically to receptor sites, attach to proteins usually clustered in coated pits on the cell surface and are carried into the cell when a vesicle forms.

■ INTERACTIVE QUESTION 7.10

a. How is cholesterol, which is used for the synthesis of other steroids and membranes, transported into human cells?

b. Explain why cholesterol accumulates in the blood of individuals with the disease familial hypercholesteremia.

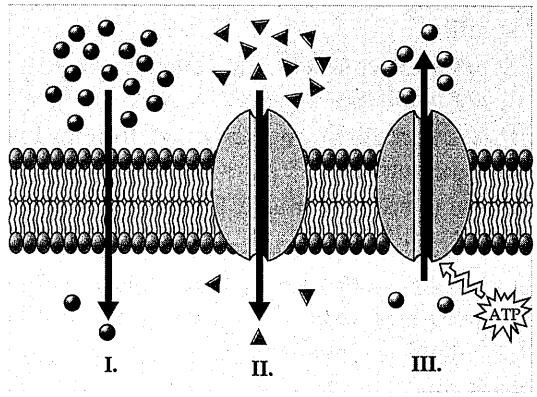
Word Roots

amphi- = dual (*amphipathic molecule:* a molecule that has both a hydrophobic and a hydrophilic region)
aqua- = water; **-pori** = a small opening (*aquaporin:* a transport protein in the plasma membrane of a plant or animal cell that specifically facilitates the diffusion of water across the membrane)
co- = together; **trans-** = across (*cotransport:* the coupling of the "downhill" diffusion of one substance to the "uphill" transport of another against its own concentration gradient)
electro- = electricity; **-genic** = producing (*electrogenic pump:* an ion transport protein generating voltage across a membrane)
endo- = inner; **cyto-** = cell (*endocytosis:* the movement of materials into a cell; celleating)
exo- = outer (*exocytosis:* the movement of materials out of a cell)
hyper- = exceeding; **-tonus** = tension (*hypertonic:* a solution with a higher concentration of solutes)
hypo- = lower (*hypotonic:* a solution with a lower concentration of solutes)
iso- = same; (*isotonic:* solutions with equal concentrations of solutes)
phago- = eat (*phagocytosis:* cell eating)
pino- = drink (*pinocytosis:* cell drinking)
plasm- = molded; **-lyso** = loosen (*plasmolysis:* a phenomenon in walled cells in which the cytoplasm shrivels and the plasma membrane pulls away from the cell wall when the cell loses water to a hypertonic environment)

Structure Your Knowledge

1. Create a concept map to illustrate your understanding of osmosis. This exercise will help you practice using the words *hypotonic, isotonic,* and *hypertonic,* and it will help you focus on the effect of these osmotic environments on plant and animal cells. Explain your map to a friend.

2. The following diagram illustrates passive and active transport across a plasma membrane. Use it to answer questions a–d.



a. Which section represents facilitated diffusion? How can you tell?
Does the cell expend energy in this transport? Why or why not?
What types of solute molecules may be moved by this type of transport?
b. Which section shows active transport?
List two ways that you can you tell?
c. Which section shows diffusion?
What types of solute molecules may be moved by this type of transport?
d. Which of these sections are considered passive transport?

Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. Glycoproteins and glycolipids are important for
   a. facilitated diffusion.
   b. active transport.
   c. cell-cell recognition.
   d. cotransport.
   e. signal-transduction pathways.

2. A single layer of phospholipid molecules coats the water in a beaker. Which part of the molecules will face the air?
   a. the phosphate groups
   b. the hydrocarbon tails
   c. both head and tail because the molecules are amphipathic and will lie sideways
   d. the phospholipids would dissolve in the water and not form a membrane coat
   e. the glycolipid regions

3. Which of the following is *not* true about osmosis?
   a. It is a passive process in cells without walls, but an active one in cells with walls.
   b. Water moves from a hypotonic to a hypertonic solution.
   c. Solute molecules bind to water and decrease the water available to move.
   d. It often occurs through channel proteins known as aquaporins.
   e. There is no net osmosis between isotonic solutions.
4. Support for the fluid mosaic model of membrane structure comes from
   a. the freeze-fracture technique of electron microscopy.
   b. the movement of proteins in hybrid cells.
   c. the amphipathic nature of many membrane proteins.
   d. both a and c.
   e. all of the above.
5. A freshwater *Paramecium* is placed into salt water. Which of the following events would occur?
   a. an increase in the action of its contractile vacuole
   b. swelling of the cell until it becomes turgid
   c. swelling of the cell until it lyses
   d. shriveling of the cell
   e. diffusion of salt ions out of the cell
6. Ions diffuse across membranes down their
   a. electrochemical gradient.
   b. electrogenic gradient.
   c. electrical gradient.
   d. concentration gradient.
   e. osmotic gradient.
7. The fluidity of membranes in a plant in cold weather may be maintained by
   a. increasing the number of phospholipids with saturated hydrocarbon tails.
   b. activating an H^+ pump.
   c. increasing the concentration of cholesterol in the membrane.
   d. increasing the proportion of peripheral proteins.
   e. increasing the number of phospholipids with unsaturated hydrocarbon tails.
8. A plant cell placed in a hypotonic environment will
   a. plasmolyze.
   b. shrivel.
   c. become turgid.
   d. become flaccid.
   e. lyse.
9. Which of the following is *not* true of the carrier molecules involved in facilitated diffusion?
   a. They increase the speed of transport across a membrane.
   b. They can concentrate solute molecules on one side of the membrane.
   c. They may have specific binding sites for the molecules they transport.
   d. They may undergo a conformational change upon binding of solute.
   e. They do not require an energy investment from the cell to operate.
10. The membrane potential of a cell favors the
    a. movement of cations into the cell.
    b. movement of anions into the cell.
    c. action of an electrogenic pump.
    d. movement of sodium out of the cell.
    e. action of a proton pump.
11. Cotransport may involve
    a. active transport of two solutes through a transport protein.
    b. passive transport of two solutes through a transport protein.
    c. ion diffusion against the electrochemical gradient created by an electrogenic pump.
    d. a pump such as the Na^+-K^+ pump that moves ions in two different directions.
    e. transport of one solute against its concentration gradient in tandem with another that is diffusing down its concentration gradient.
12. Exocytosis may involve all of the following *except*
    a. ligands and coated pits.
    b. the fusion of a vesicle with the plasma membrane.
    c. a mechanism to transport carbohydrates to the outside of plant cells during the formation of cell walls.
    d. a mechanism to rejuvenate the plasma membrane.
    e. a means of exporting large molecules.
13. The proton pump in plant cells is the functional equivalent of an animal cell's
    a. cotransport mechanism.
    b. sodium-potassium pump.
    c. contractile vacuole for osmoregulation.
    d. receptor-mediated endocytosis of cholesterol.
    e. ATP pump.

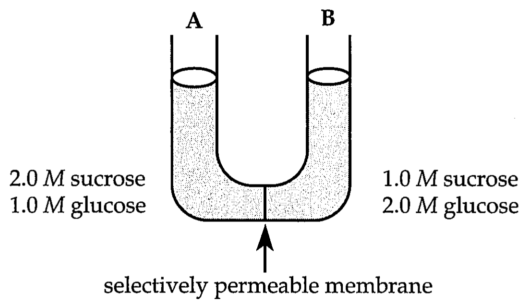
14. Pinocytosis involves
a. the fusion of a newly formed food vacuole with a lysosome.
b. receptor-mediated endocytosis and the formation of vesicles.
c. the pinching in of the plasma membrane around small droplets of external fluid.
d. pseudopod extension as vesicles move along the cytoskeleton and fuse with the plasma membrane.
e. the accumulation of specific large molecules in a cell.

15. Watering a houseplant with too concentrated a solution of fertilizer can result in wilting because
a. the uptake of ions into plant cells makes the cells hypertonic.
b. the soil solution becomes hypertonic, causing the cells to lose water.
c. the plant will grow faster than it can transport water and maintain proper water balance.
d. diffusion down the electrochemical gradient will cause a disruption of membrane potential and accompanying loss of water.
e. the plant will suffer fertilizer burn due to a caustic soil solution.

16. A cell is manufacturing receptor proteins for cholesterol. How would those proteins be oriented in the following membranes before they reach the plasma membrane?
a. facing inside the ER lumen but outside the transport vesicle membrane
b. facing inside the ER lumen and inside the transport vesicle
c. attached outside the ER and outside the transport vesicle
d. attached outside the ER but facing inside the transport vesicle
e. completely embedded in the hydrophobic center of both the ER and transport vesicle membranes

17. Which of the following is the most probable description of an integral, transmembrane protein?
a. amphipathic with a hydrophilic head and a hydrophobic tail region
b. a globular protein with hydrophobic amino acids in the interior and hydrophilic amino acids arranged around the outside
c. a fibrous protein coated with hydrophobic sugar residues
d. a glycolipid attached to the portion of the protein facing the exterior of the cell and cytoskeletal elements attached to the portion facing inside the cell
e. a middle region composed of α-helical stretches of hydrophobic amino acids, with hydrophilic regions at both ends of the protein

Use the U-tube setup to answer questions 18 through 20.



The solutions in the two arms of this U-tube are separated by a membrane that is permeable to water and glucose but not to sucrose. Side A is filled with a solution of 2.0 *M* sucrose and 1.0 *M* glucose. Side B is filled with 1.0 *M* sucrose and 2.0 *M* glucose.

18. *Initially,* the solution in side A, with respect to that in side B,
a. has a lower solute concentration.
b. has a higher solute concentration.
c. has an equal solute concentration.
d. is lower in the tube.
e. is higher in the tube.

19. During the period *before* equilibrium is reached, which molecule(s) will show net movement through the membrane?
a. water
b. glucose
c. sucrose
d. water and sucrose
e. water and glucose

20. *After* the system reaches equilibrium, what changes are observed?
a. The water level is higher in side A than in side B.
b. The water level is higher in side B than in side A.
c. The molarity of glucose is higher in side A than in side B.
d. The molarity of sucrose has increased in side A.
e. Both a and c have occurred.

21. Facilitated diffusion across a cellular membrane requires ________ and moves a solute ________ its concentration gradient. (Assume solute is not an ion.)
    - **a.** energy and transport proteins . . . down
    - **b.** energy and transport proteins . . . up (against)
    - **c.** energy . . . up
    - **d.** transport proteins . . . down
    - **e.** transport proteins . . . up

22. The extracellular fluids that surround the cells of a multicellular animal must be ________ to the cells.
    - **a.** buffers
    - **b.** isotonic
    - **c.** hypotonic
    - **d.** hypertonic
    - **e.** homeostatic

23. LDLs (low-density lipoproteins) enter animal cells by
    - **a.** diffusion through the lipid bilayer.
    - **b.** pinocytosis.
    - **c.** exocytosis.
    - **d.** receptor-mediated endocytosis.
    - **e.** diffusion through transport proteins

24. The fluid mosaic model describes biological membranes as consisting of
    - **a.** a phospholipid bilayer with proteins sandwiched between the layers.
    - **b.** a lipid bilayer with proteins coating the outside of this hydrophobic structure.
    - **c.** a phospholipid bilayer with proteins embedded in and attached to it.
    - **d.** a protein bilayer with phospholipids embedded in it.
    - **e.** a cholesterol bilayer with proteins embedded in the hydrophobic center.

25. You observe plant cells under a microscope that have just been placed in an unknown solution. First the cells plasmolyze; after a few minutes, the plasmolysis reverses and the cells appear normal. What would you conclude about the unknown solute.
    - **a.** It is hypertonic to the plant cells, and its solute cannot cross the plant cell membranes.
    - **b.** It is hypotonic to the plant cells, and its solute cannot cross the plant cell membranes.
    - **c.** It is isotonic to the plant cells, but its solute can cross the plant cell membranes.
    - **d.** It is hypertonic to the plant cells, but its solute can cross the plant cell membranes.
    - **e.** It is hypotonic to the plant cells, but its solute can cross the plant cell membranes.