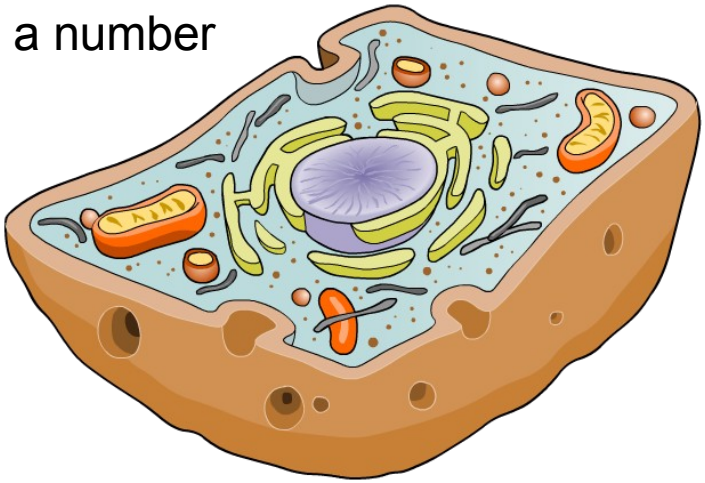
What are membranes?

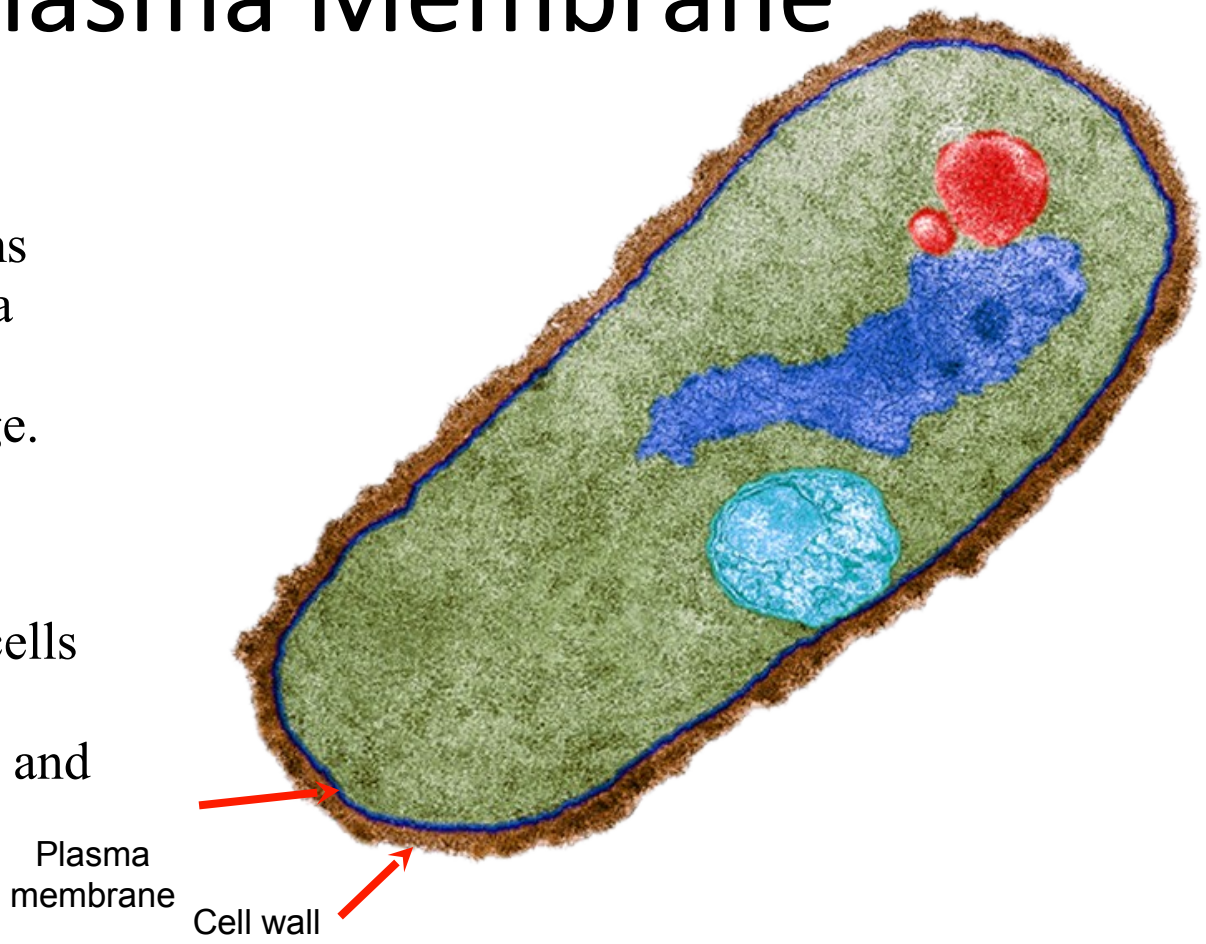
Membranes cover the surface of every cell, and also surround most organelles within cells. They have a number of functions, such as:



- keeping all cellular components inside the cell
- allowing selected molecules to move in and out of the cell
- isolating organelles from the rest of the cytoplasm, allowing cellular processes to occur separately.
- a site for biochemical reactions
- allowing a cell to change shape.

The Plasma Membrane

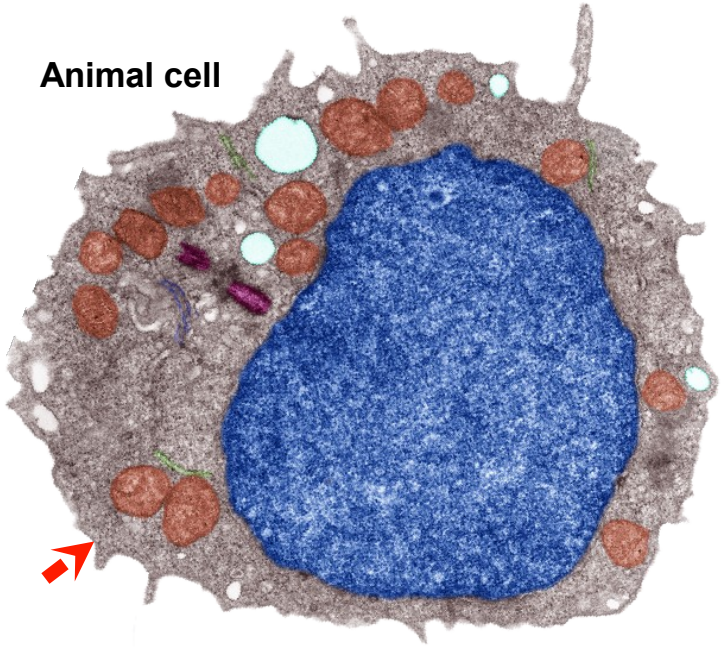
- A **plasma membrane** is common to all cells.It forms their **outer limit**. It forms a boundary for dissolved substances-allows exchange. Allows cells to maintain themselves
- Bacteria, fungi, and plant cells have a **cell wall**, but it is a structurally distinct feature and lies outside the plasma membrane.

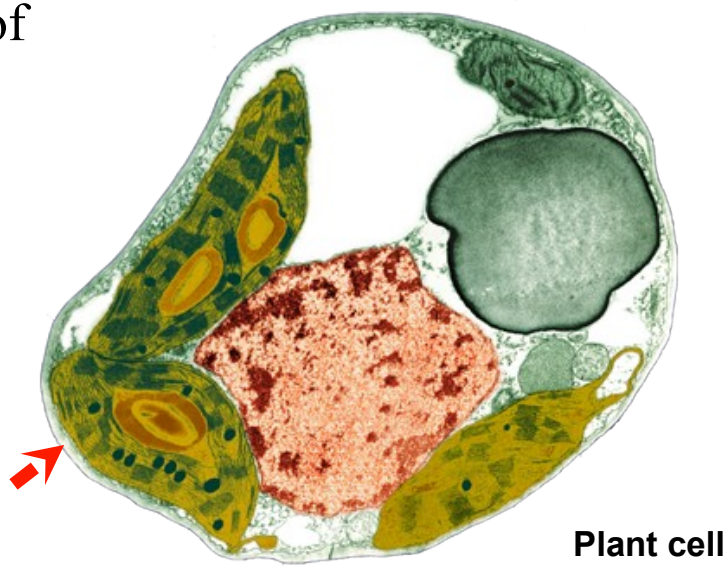


This colored *Bacillus megaterium* cell clearly shows the plasma membrane, which lies inside the distinct structure of the cell wall.

Cells and Membranes

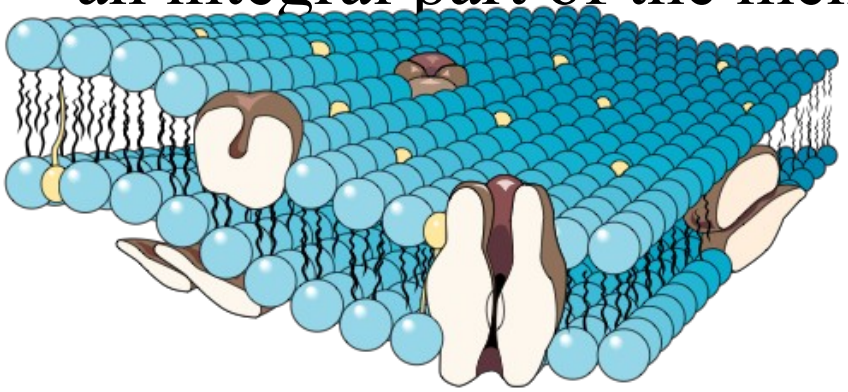
- The membrane surrounding a cell, called the **plasma membrane**, forms the boundary that separates the living cell from its non-living surroundings.
- Although the plasma membrane (arrowed) is only about 8 nm (0.01 micrometere) thick, it:
  - selectively controls the movement of materials into and out of the cell (selectively permeable)
  - is responsible for cell-cell recognition (e.g. when cells aggregate into tissues
  - is a dynamic structure, with distinct inside and outside faces.

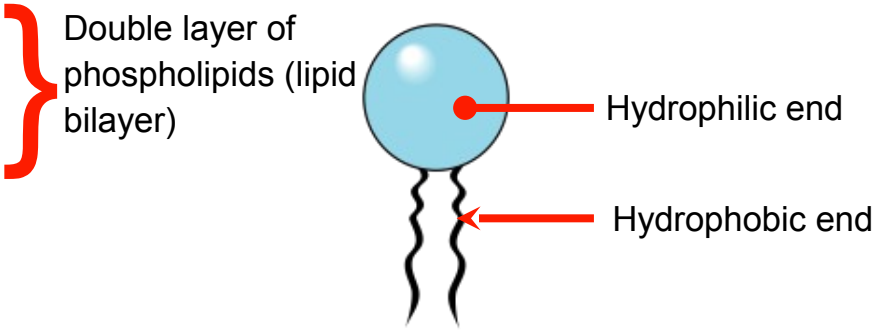




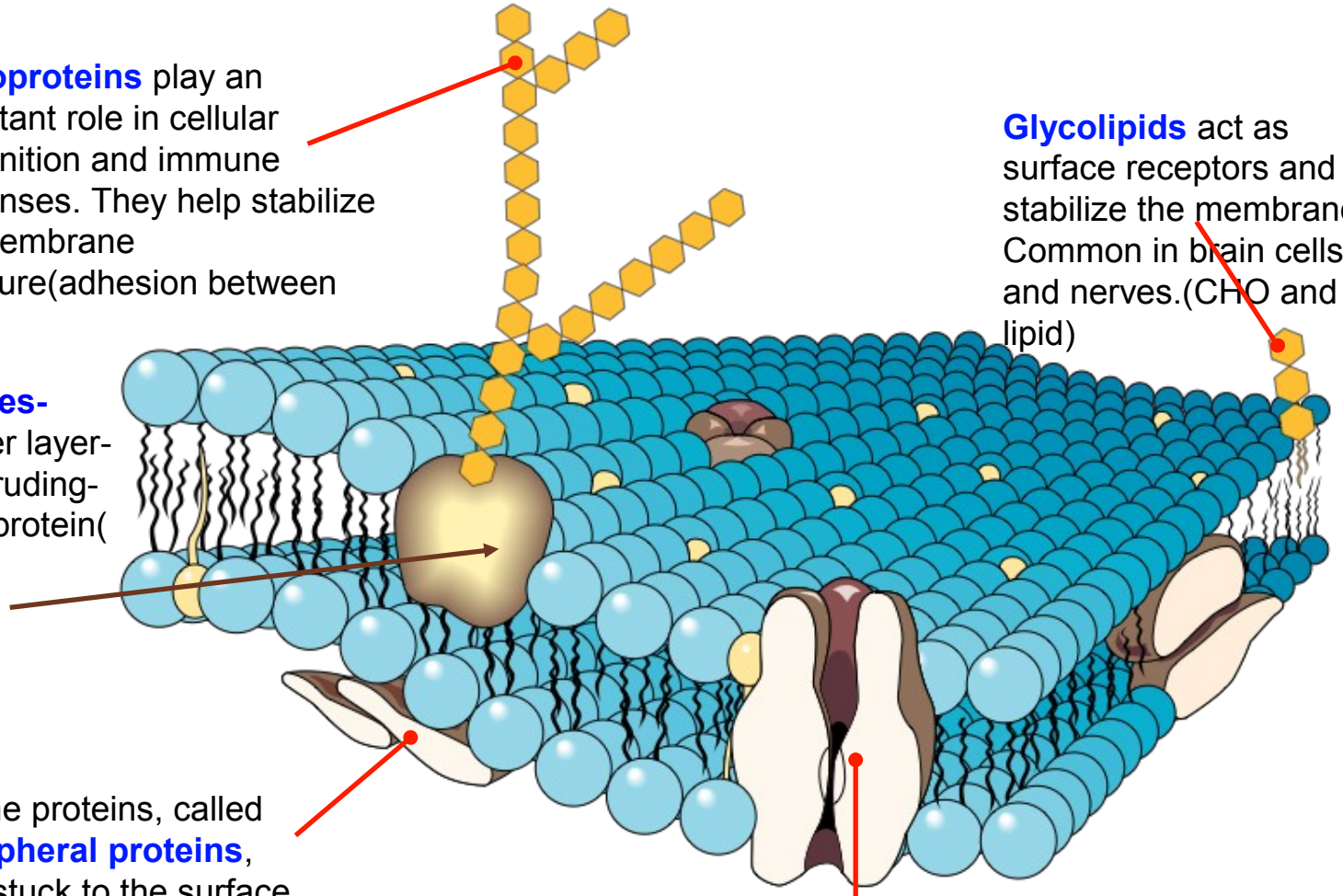
Membrane Structure

- The currently accepted model for the structure of the **plasma membrane** (and cellular membranes generally) is the **fluid mosaic model**.
  - In this model there is a double layer of **phospholipids** (fats), which are arranged with their **hydrophobic tails** facing inwards.(repel water)
  - The **hydrophilic head** (phosphate) is attracted to water-both inside and outside cell-cell is in a watery environment
  - The double layer of lipids is quite **fluid**, with **proteins** floating within it.
  - Glycoproteins, glycolipids, and cholesterol are also an integral part of the membrane structure.





Membrane Structure



Glycoproteins play an important role in cellular recognition and immune responses. They help stabilize the membrane structure(adhesion between cells)

Glycolipids act as surface receptors and stabilize the membrane. Common in brain cells and nerves.(CHO and lipid)

Carbohydrates- found on outer layer- linked to protruding- protein(glycoprotein(

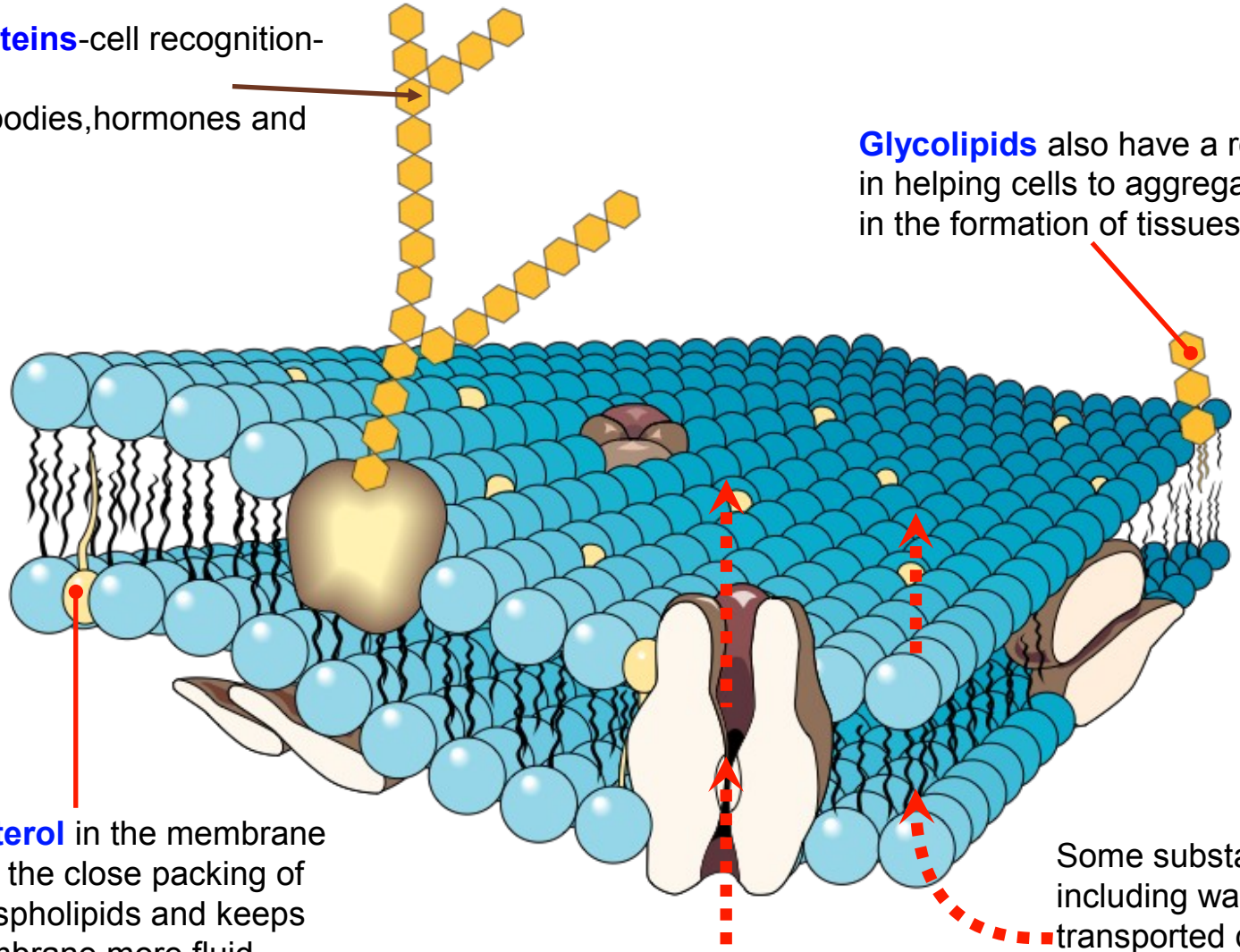
Some proteins, called **peripheral proteins**, are stuck to the surface of the membrane.

Some proteins completely penetrate the phospholipid layer. These proteins may control the movement of specific molecules into and out of the cell.

Membrane Structure

Glycoproteins-cell recognition-between cells,antibodies,hormones and viruses

Glycolipids also have a role in helping cells to aggregate in the formation of tissues.



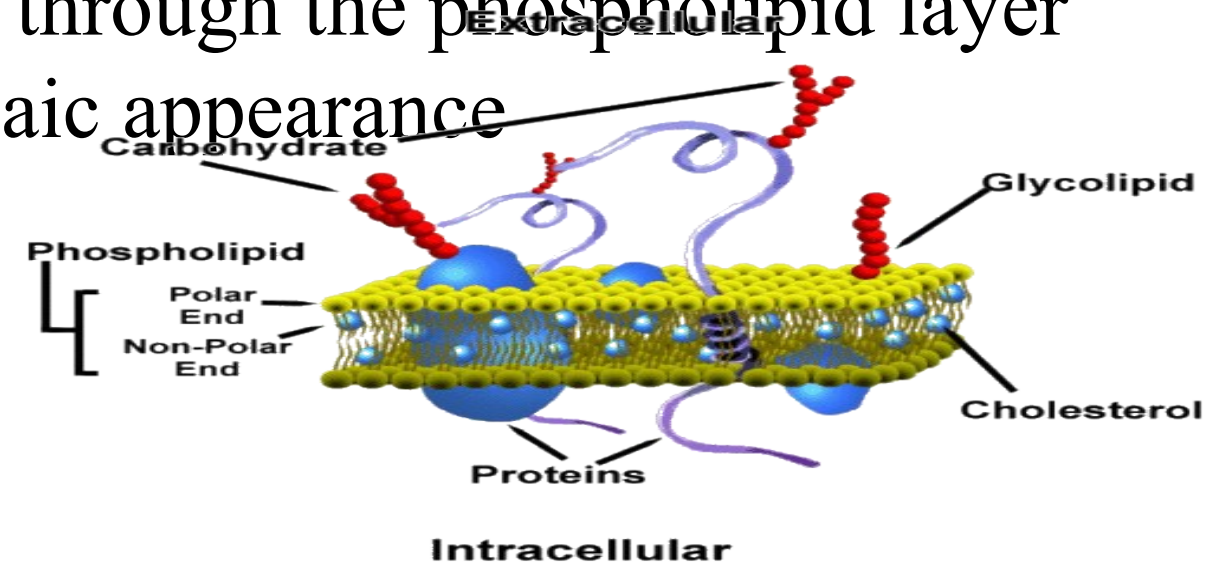
Cholesterol in the membrane disturbs the close packing of the phospholipids and keeps the membrane more fluid. Provides rigidity and water resistance. Membranes would break down without it. Plants have phytosterol.

Some substances, particularly ions and carbohydrates, are transported across the membrane via the proteins.

Some substances, including water, are transported directly through the **phospholipid bilayer**. **But mostly impermeable to water soluble(polar) molecules-most movement via proteins.**

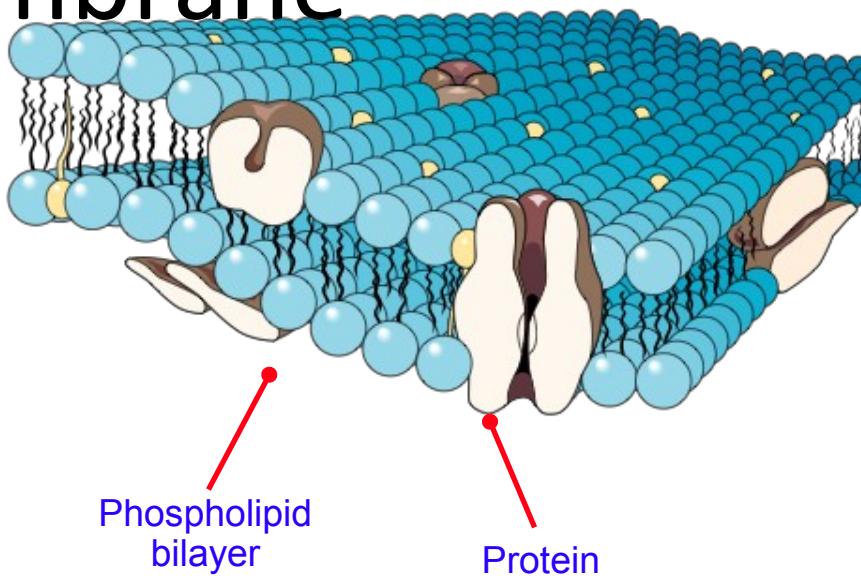
Fluid –Mosaic model

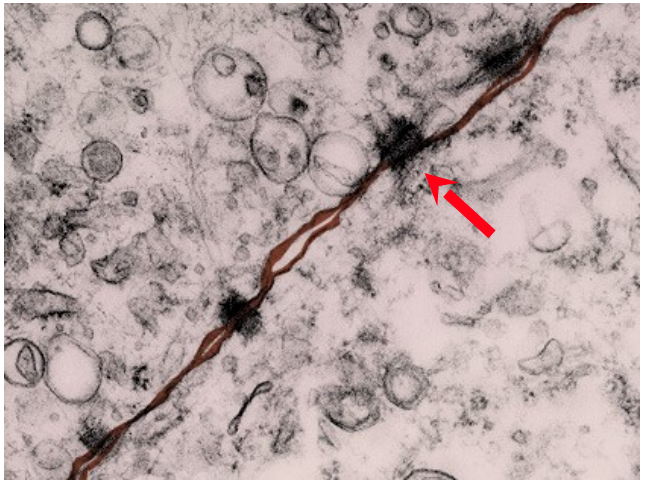
- **Fluid**- individual phospholipids and some proteins can move sideways(laterally) in each layer-therefore FLUID
- **Mosaic**-range of different proteins resting on the surface or through the phospholipid layer gives it a mosaic appearance



Plasma Membrane

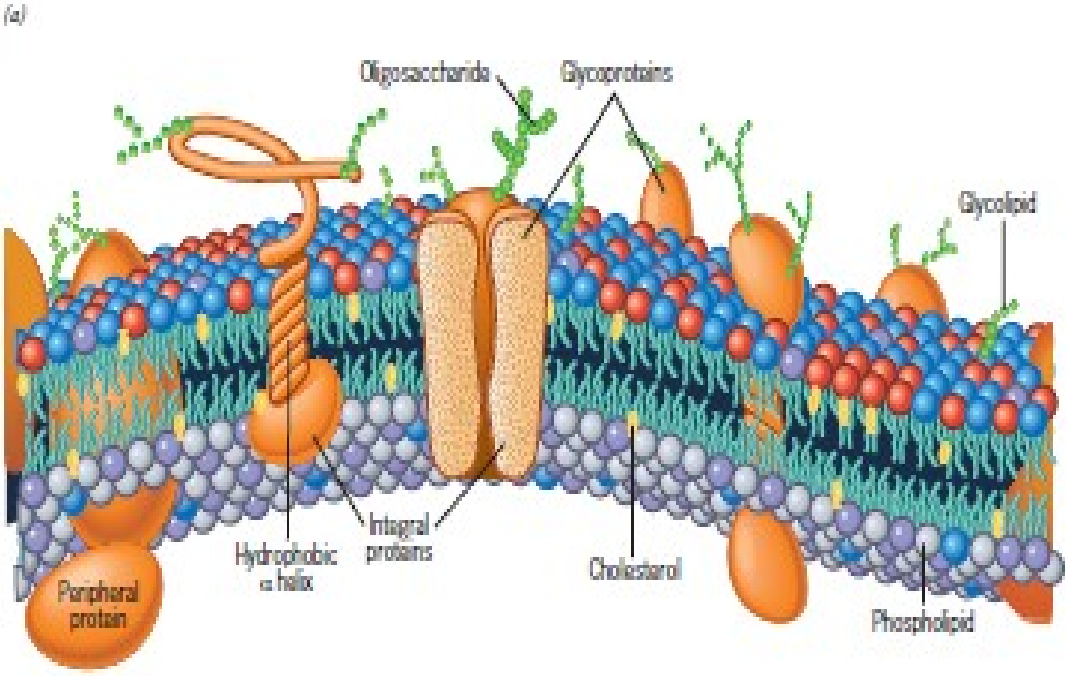
- **Located**: Surrounds the cell forming a boundary between the cell contents and the extracellular environment.
- **Structure**: Semi-fluid phospholipid bilayer in which proteins are embedded. Some of the proteins fully span the membrane.
- **Function**:
  - Forms the boundary between the cell and the extracellular environment.
  - Regulates movement

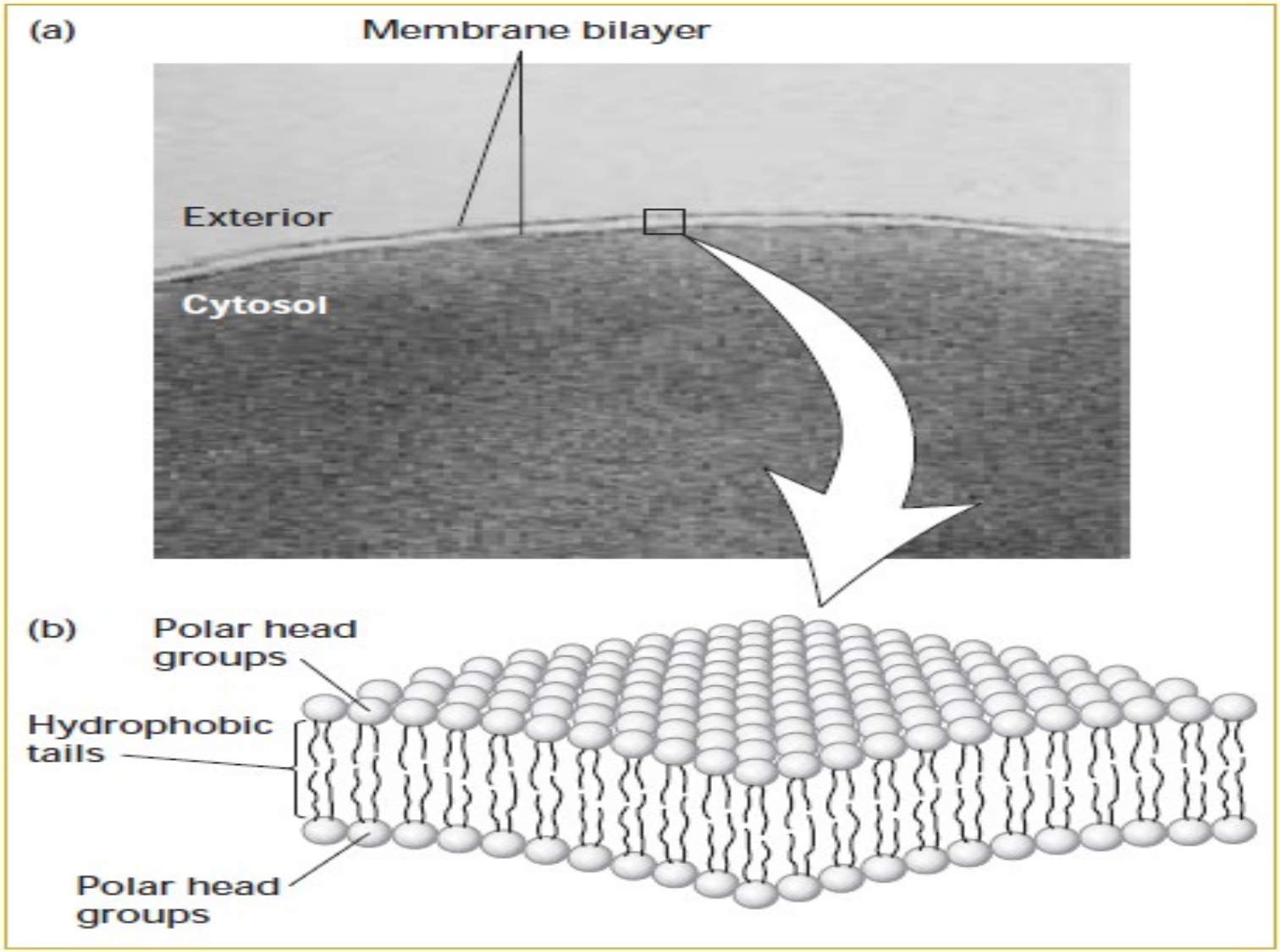




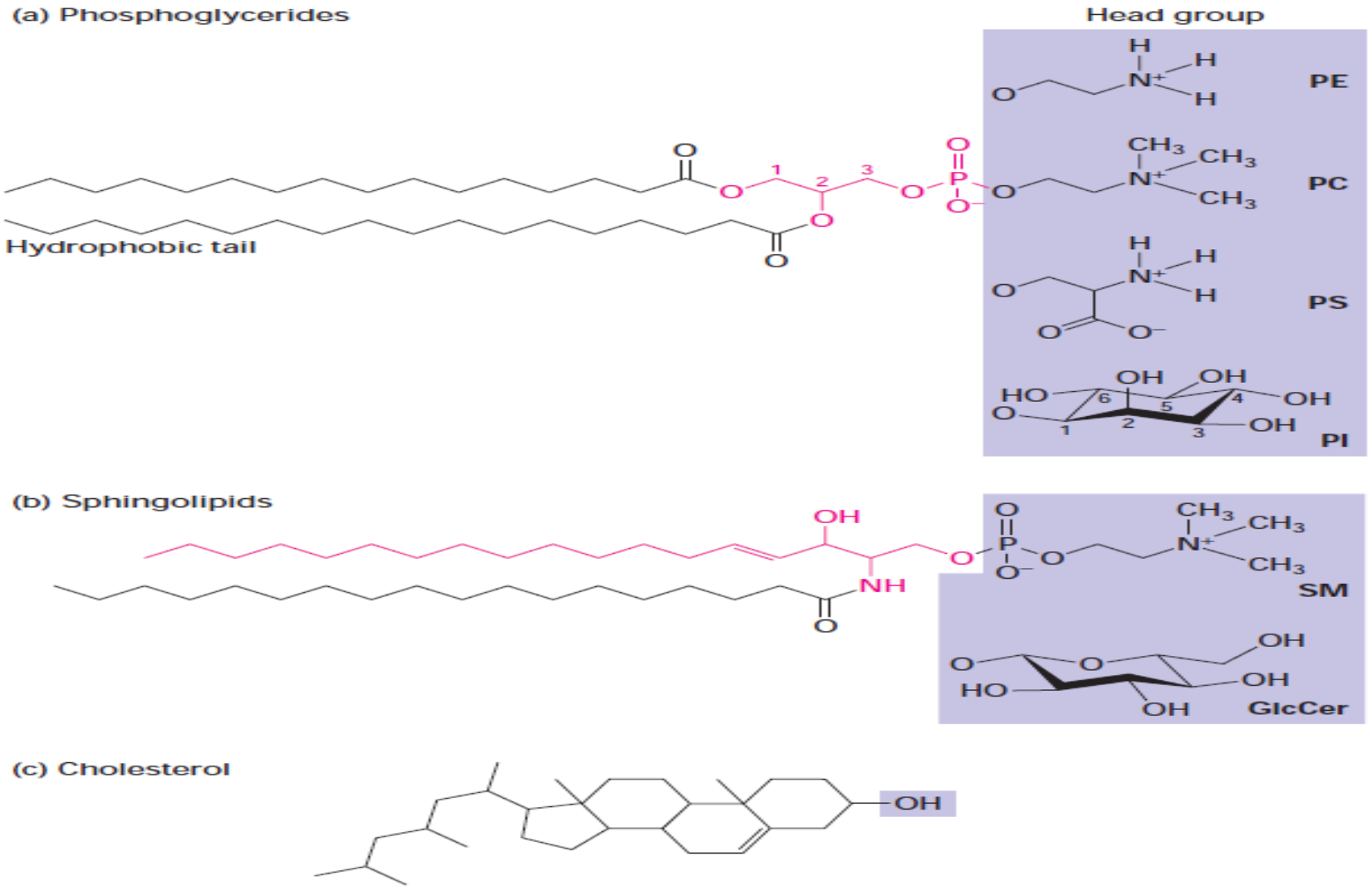
The plasma membranes of two adjacent cells joined with **desmosomes**

PLASMA MEMBRANE




(a)
Membrane bilayer
Exterior
Cytosol
(b)
Polar head groups
Hydrophobic tails
Polar head groups

THREE CLASSES OF MEMBRANE LIPIDS



The Lipid Bilayer

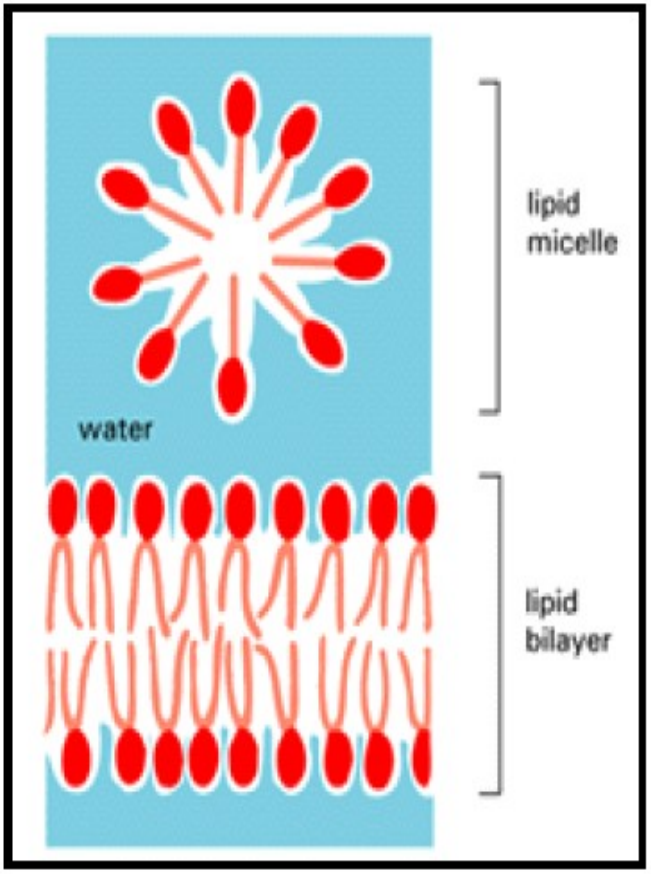
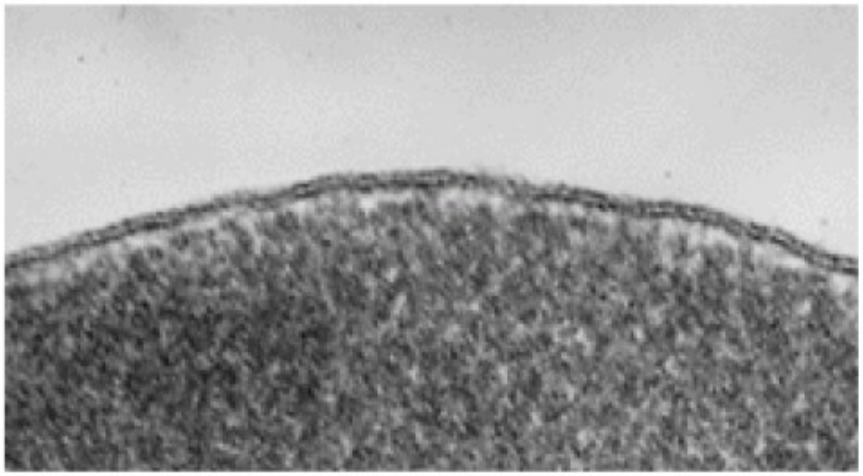
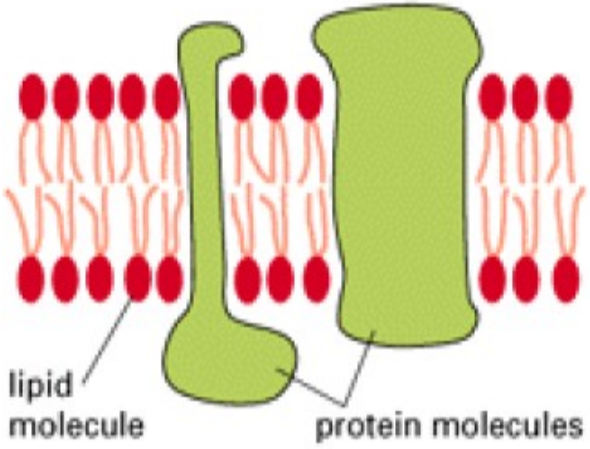


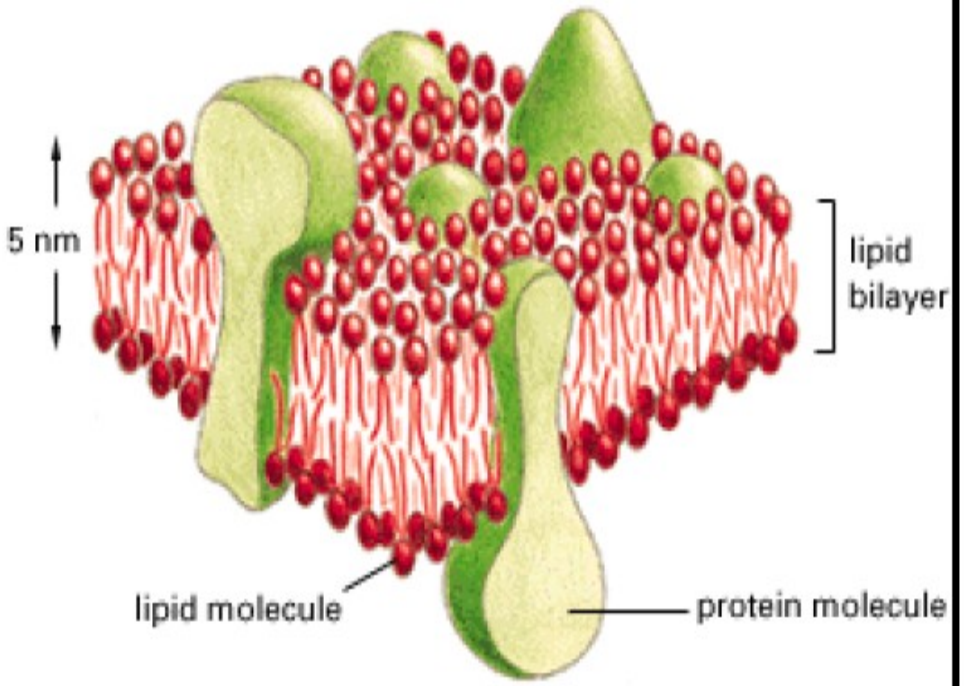
Figure 10-3. A lipid micelle and a lipid bilayer seen in cross-section. Lipid molecules form such structures spontaneously in water. The shape of the lipid molecule determines which of these structures is formed. Wedge-shaped lipid molecules (*above*) form micelles, whereas cylinder-shaped phospholipid molecules (*below*) form bilayers.



(A)



(B)



(C)

Figure 10-1. Three views of a cell membrane. (A) An electron micrograph of a plasma membrane (of a human red blood cell) seen in cross-section. (B and C) Schematic drawings showing two-dimensional and three-dimensional views of a cell membrane. (A, courtesy of Daniel S. Friend.)

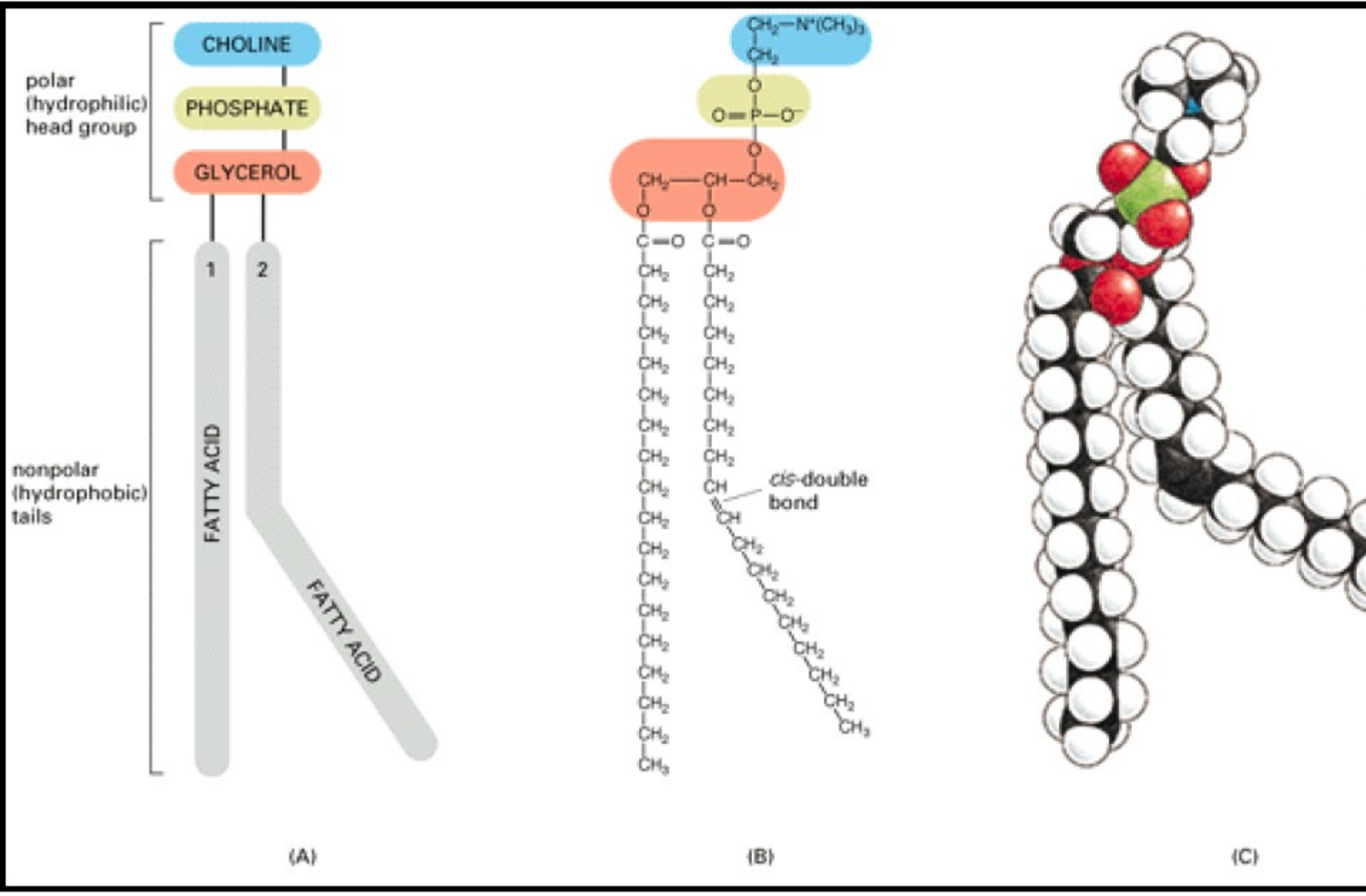
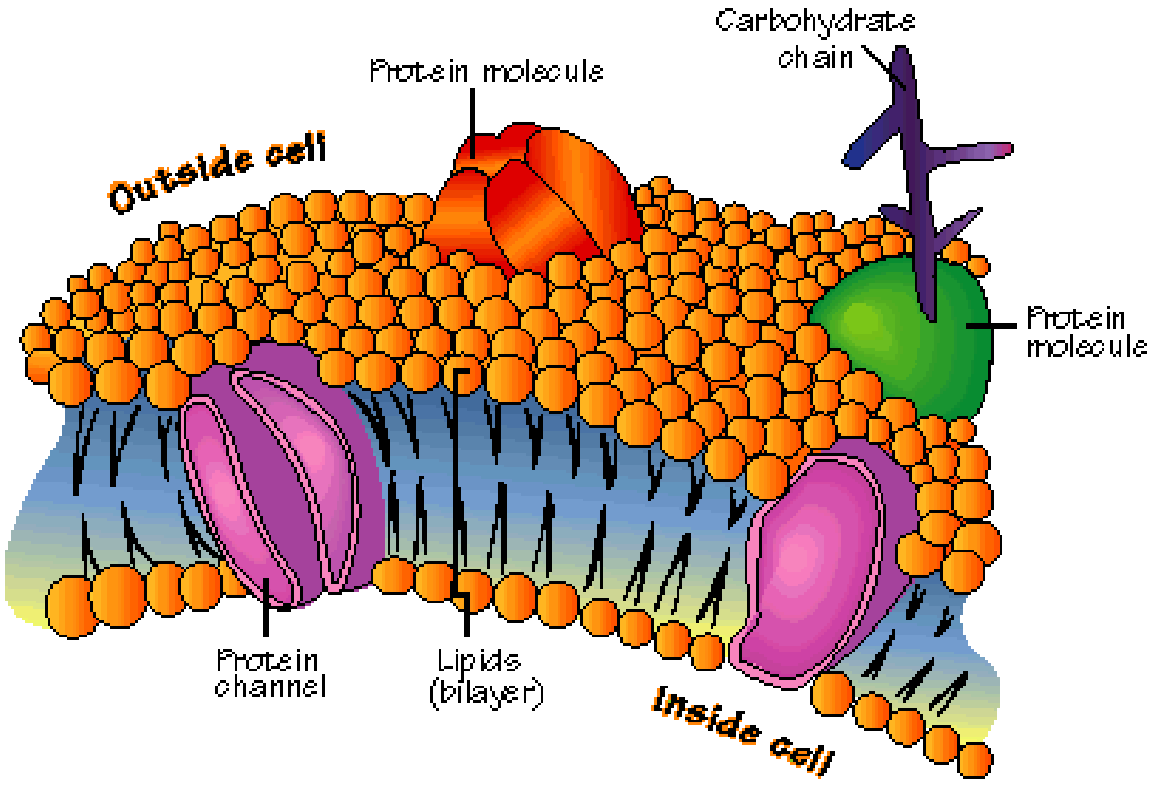


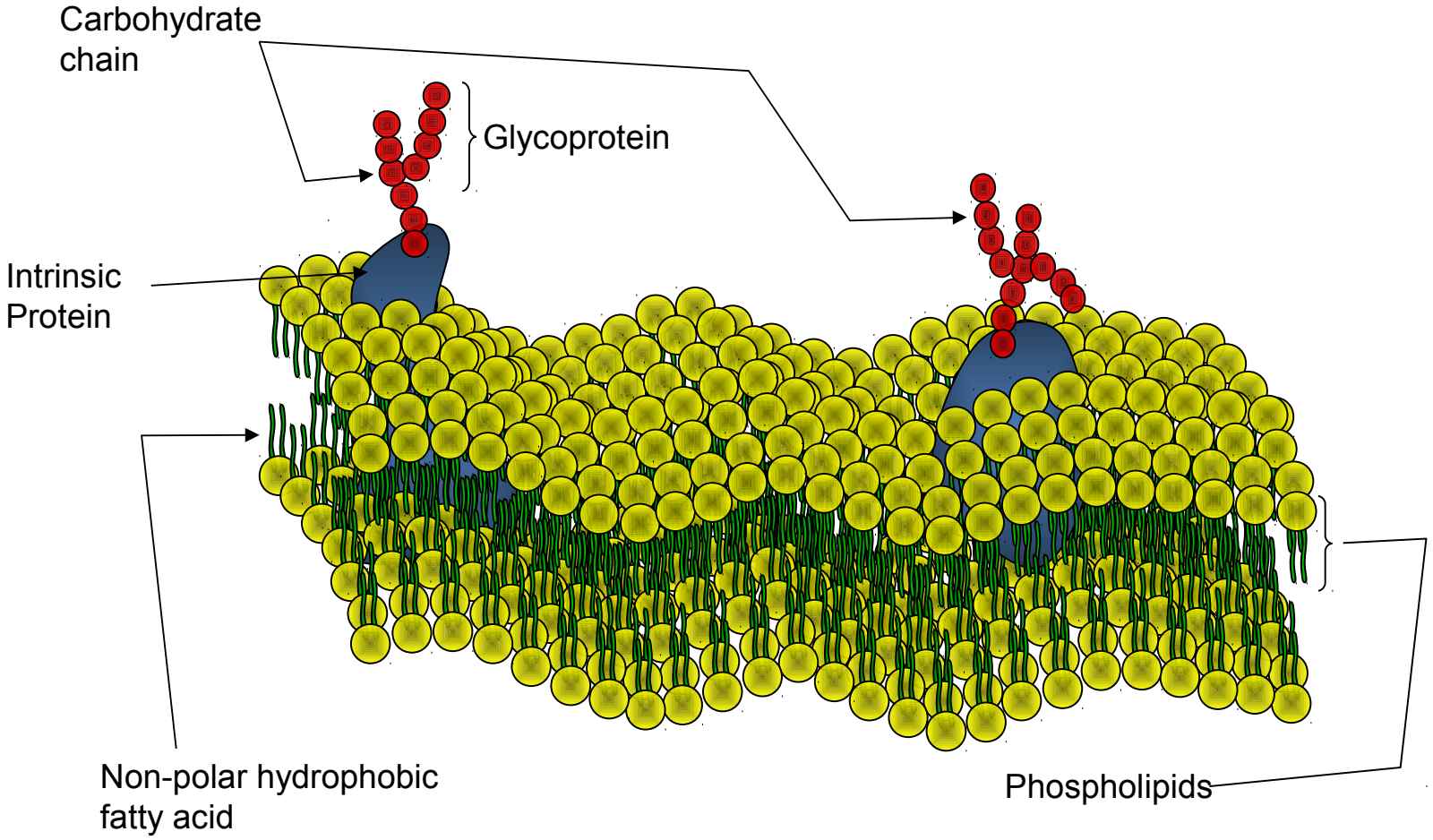
Figure 10-2. The parts of a phospholipid molecule. Phosphatidylcholine, represented schematically (A), in formula (B), as a space-filling model (C), and as a symbol (D). The k

- ***Plasma Membrane***

- A lipid/protein/carbohydrate complex, providing a barrier and containing transport and signaling systems.



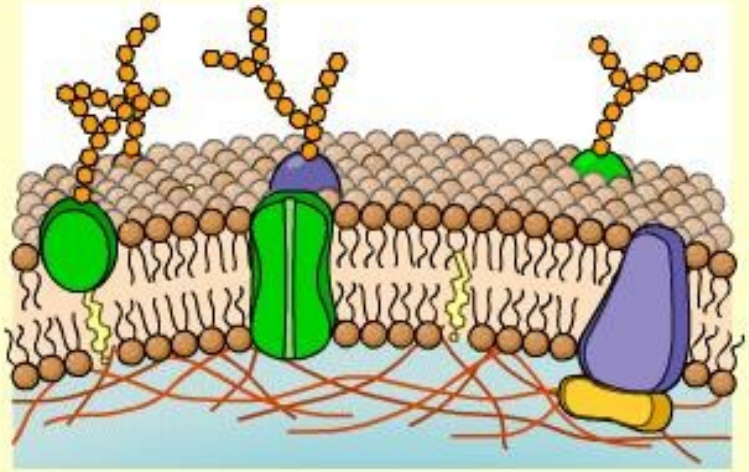
Fluid Mosaic Model of the Plasma Membrane



Membranes: timeline of discovery

The discovery of the structure of the cell membrane

Click on the dates on the timeline to find out more details about how the structure of the cell membrane was discovered.

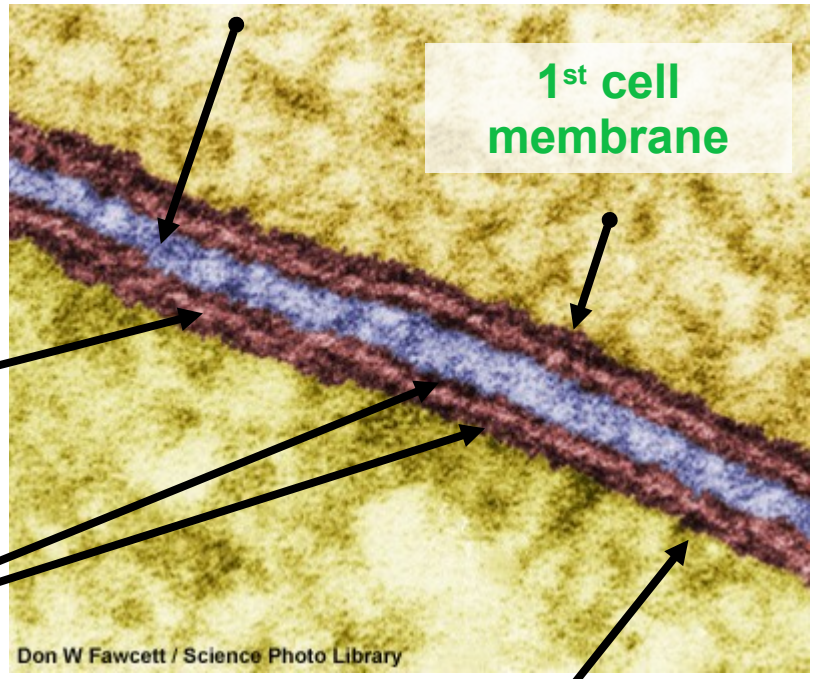


1895 — 1917 — 1925 — 1935 — 1972

Evidence for the Davson–Danielli model

When clear electron micrographs of membranes became available, they appeared to show support for Davson–Danielli's model, showing a three-layered structure.

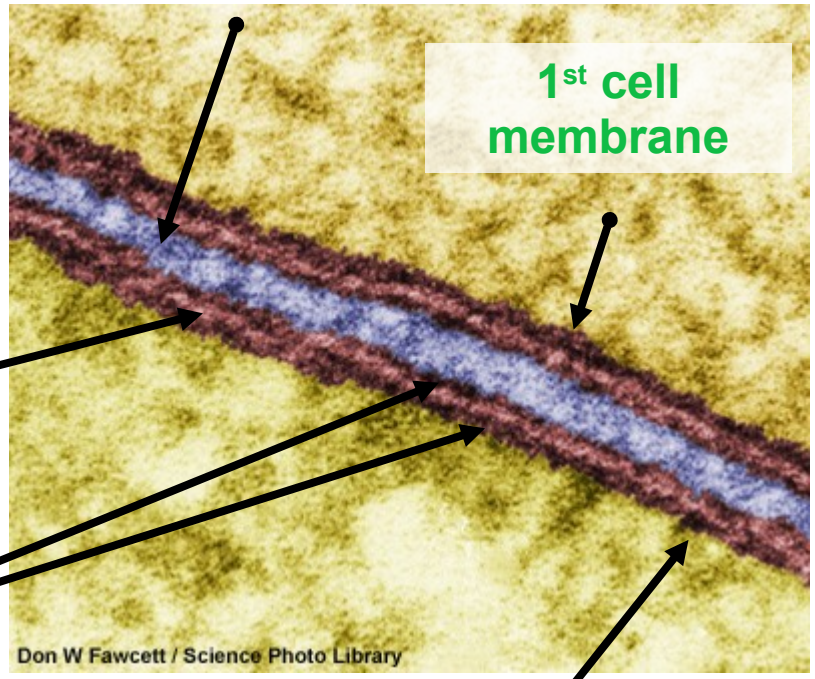
This was taken to be the phospholipid bilayer (light) surrounded by two layers of protein (dark).



Evidence for the Davson–Danielli model

Later, it was discovered that the light layer represented the phospholipid tails and the dark layers represented the phospholipid heads.

intracellular space (blue)



1 light layer = phospholipid tails

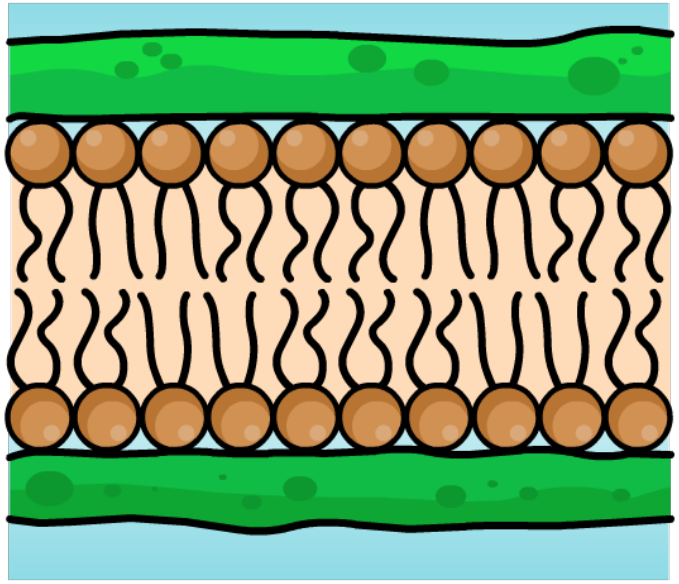
2 dark layers: phospholipid heads

2nd cell membrane

Problems with the Davson–Danielli model

By the end of the 1960s, new evidence cast doubts on the viability of the Davson–Danielli model.

- The amount and type of membrane proteins vary greatly between different cells.



- It was unclear how the proteins in the model would permit the membrane to change shape without bonds being broken.

- Membrane proteins are largely hydrophobic and therefore should not be found where the model positioned them: in the aqueous cytoplasm and extracellular environment.

Evidence from freeze-fracturing

In 1966, biologist Daniel Branton used freeze-fracturing to split cell membranes between the two lipid layers, revealing a 3D view of the surface texture.

This revealed a smooth surface with small bumps sticking out. These were later identified as proteins.

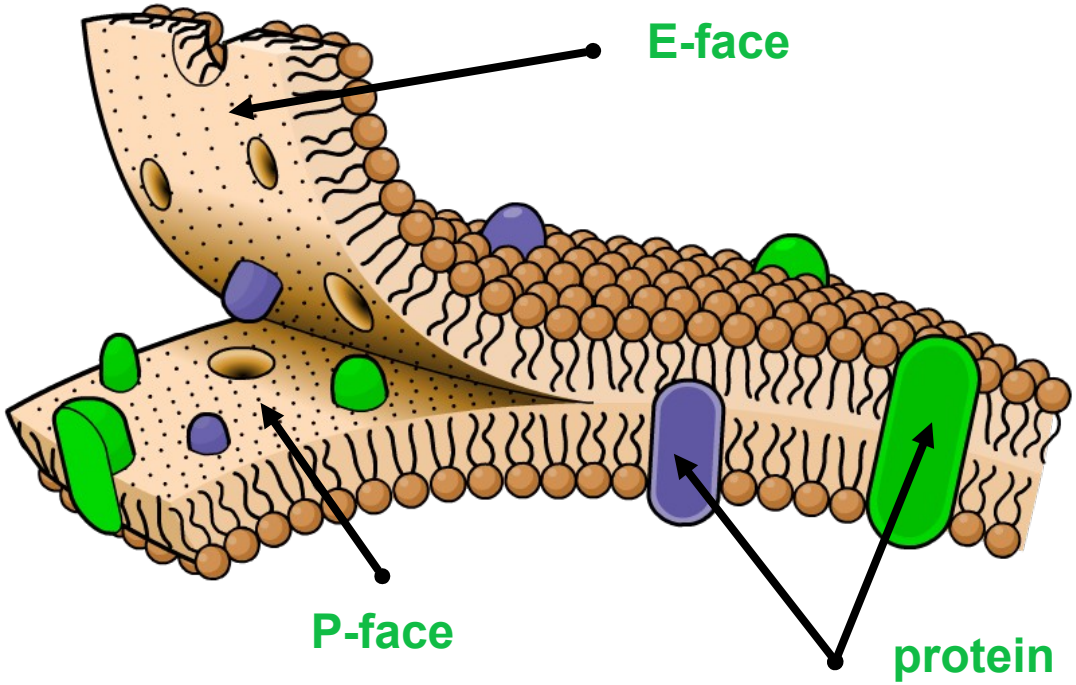
E-face: looking up at outer layer of membrane

P-face: looking down on inner layer of membrane

The fluid mosaic model

The freeze-fracture images of cell membranes were further evidence against the Davson–Danielli model.

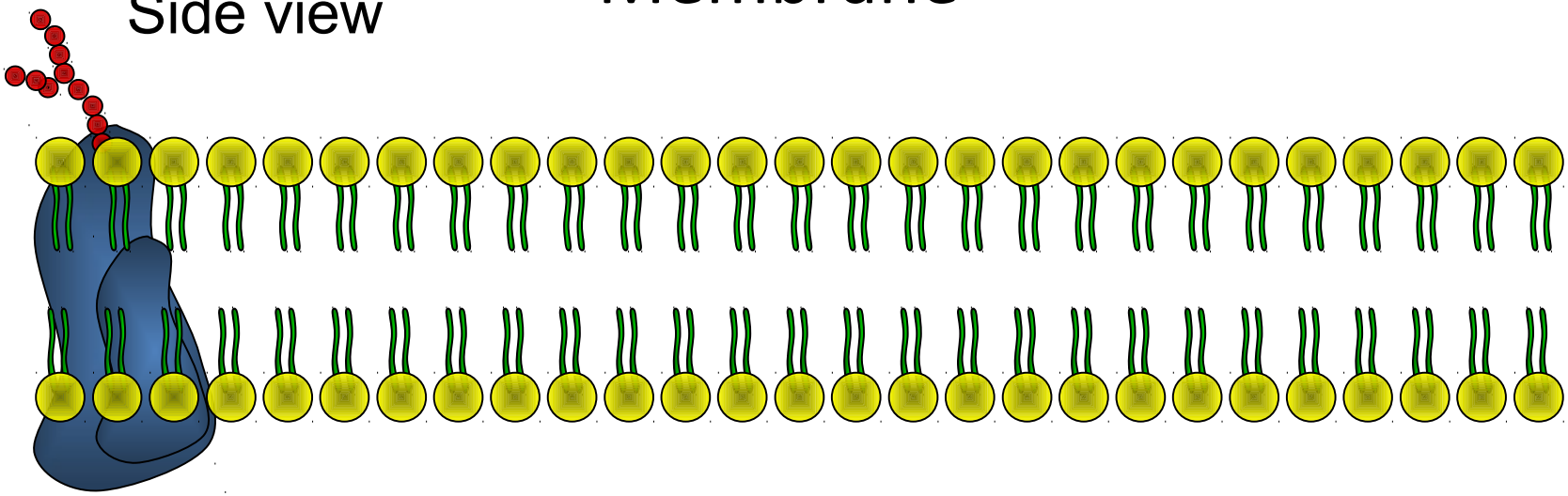
They led to the development of the **fluid mosaic model**, proposed by Jonathan Singer and Garth Nicholson in 1972.



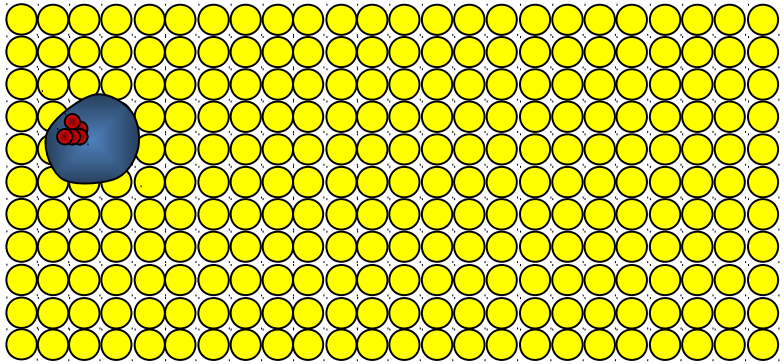
This model suggested that proteins are found **within,** not outside, the phospholipid bilayer.

Biochemical Composition of the Plasma Membrane

Side view

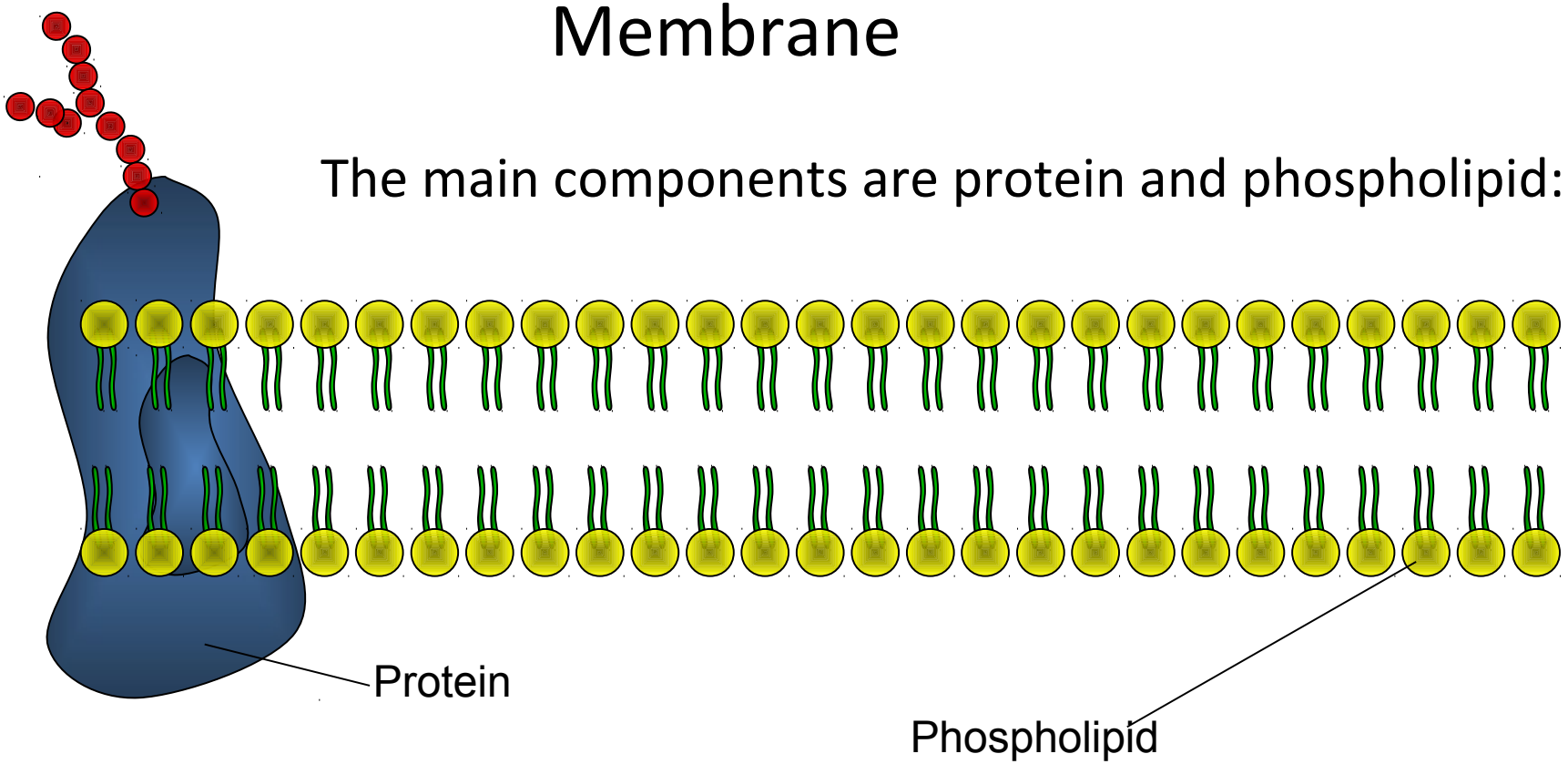


Surface view



Biochemical Composition of the Plasma Membrane

The main components are protein and phospholipid:



Side view

Membrane Structure and Function

Membrane Function

- **Membranes organize the chemical activities of cells.**
- The outer plasma membrane
  - forms a boundary between a living cell and its surroundings
  - Exhibits selective permeability
    - Controls traffic of molecules in and out

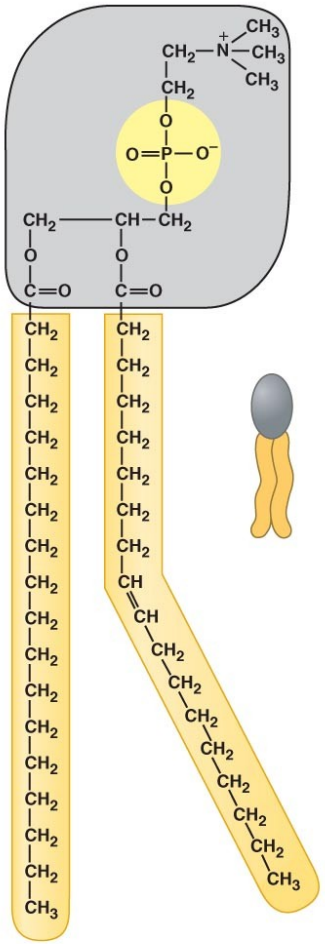
Membrane Function

- Internal membranes provide structural order for metabolism
    - Form the cell's organelles
    - Compartmentalize chemical reactions

Fluid Mosaic Model of the PM

- A membrane is a mosaic
  - Proteins and other molecules are embedded in a framework of phospholipids
- A membrane is fluid
  - Most protein and phospholipid molecules can move laterally

Membrane Structure



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Phospholipids are the major structural component of membranes.

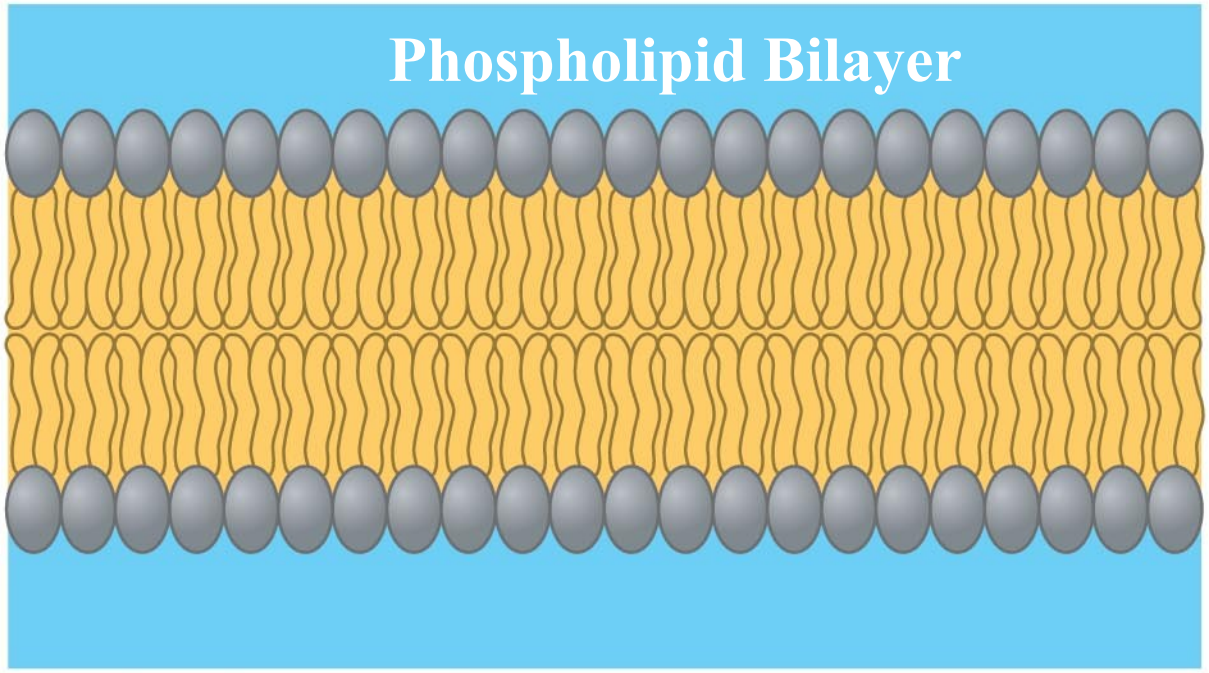
Membrane Structure

All membranes are phospholipid bilayers with embedded proteins.

Label the:

Hydrophilic heads

Hydrophobic tails



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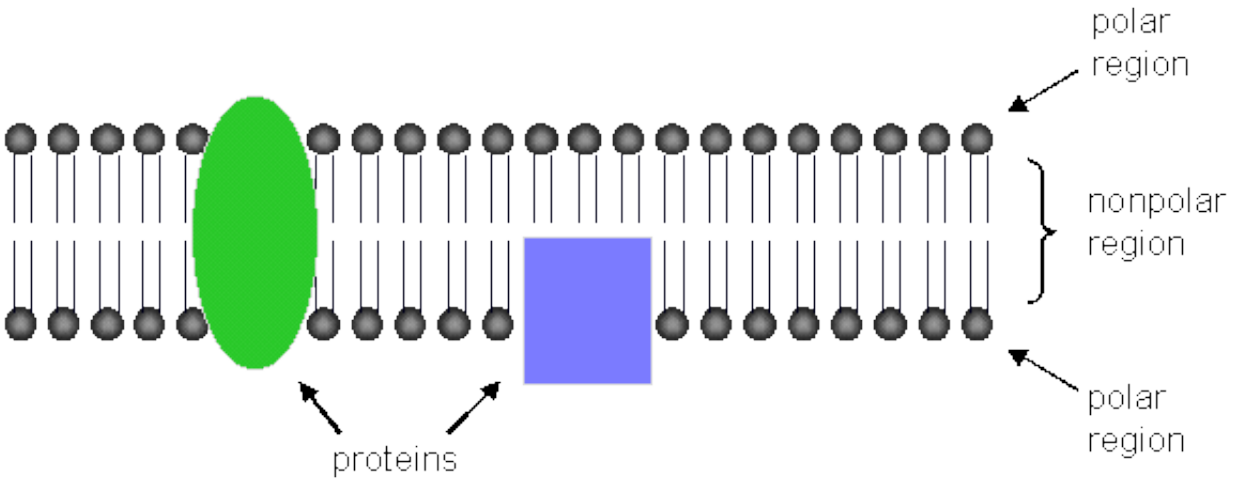
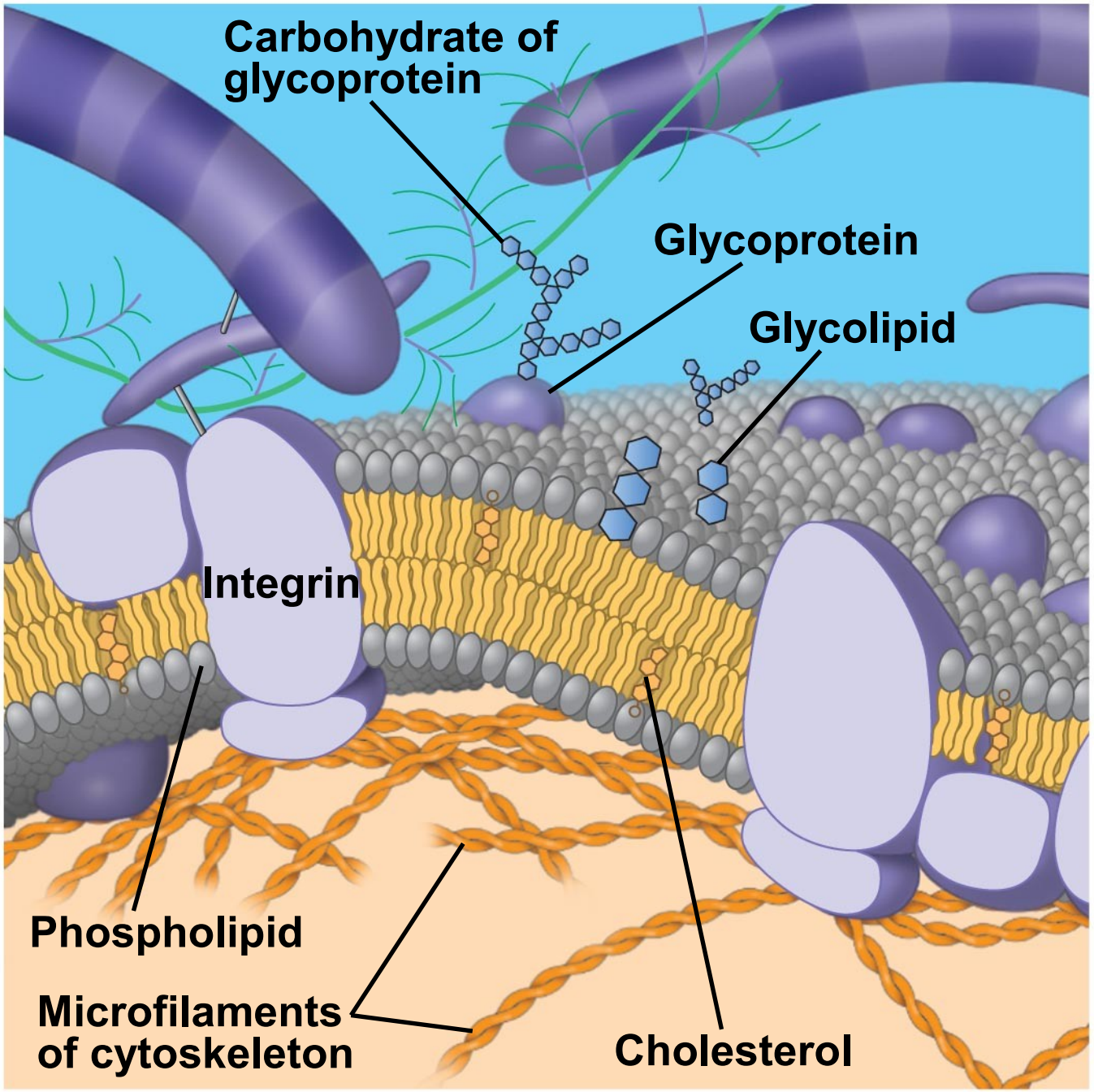
- Embedded in the bilayer are proteins
  - Most of the membrane's functions are accomplished by the embedded proteins.
    - Integral proteins span the membrane
    - Peripheral proteins are on one side or the other of the membrane



Plasma Membrane Components

- Glycoproteins and glycolipids are proteins/lipids with short chain carbohydrates attached on the extracellular side of the membrane.

Fig. 5-1a



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Types of Membrane Proteins

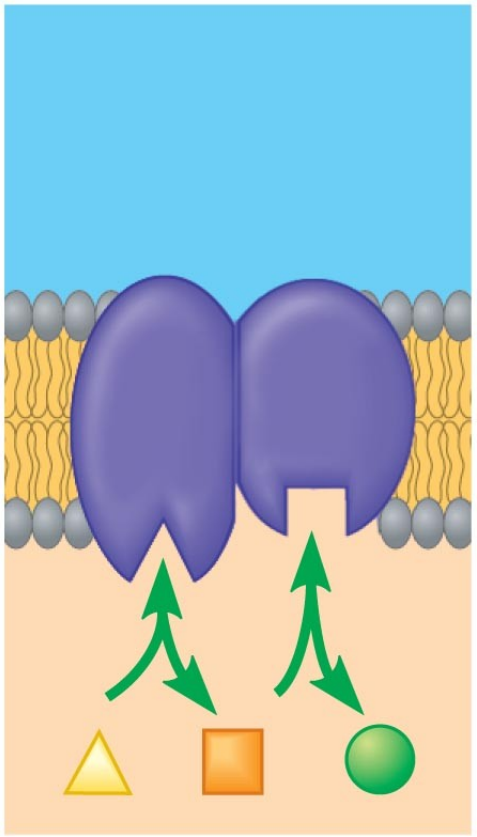
1. Cell-cell recognition proteins
2. Integrins
3. Intercellular junction proteins
4. Enzymes
5. Signal transduction proteins
   - Aka - Receptor proteins

1. Transport proteins
   - Passive and active

- Cell-cell recognition proteins - identify type of cell and identify a cell as “self” versus foreign
  - Most are glycoproteins
    - Carbohydrate chains vary between species, individuals, and even between cell types in a given individual.
    - Glycolipids also play a role in cell recognition

- Integrins are a type of integral protein
  - The cytoskeleton attaches to integrins on the cytoplasmic side of the membrane
  - Integrins strengthen the membrane
- Intercellular junction proteins - help like cells stick together to form tissues

- Many membrane proteins are enzymes
  - This is especially important on the membranes of organelles.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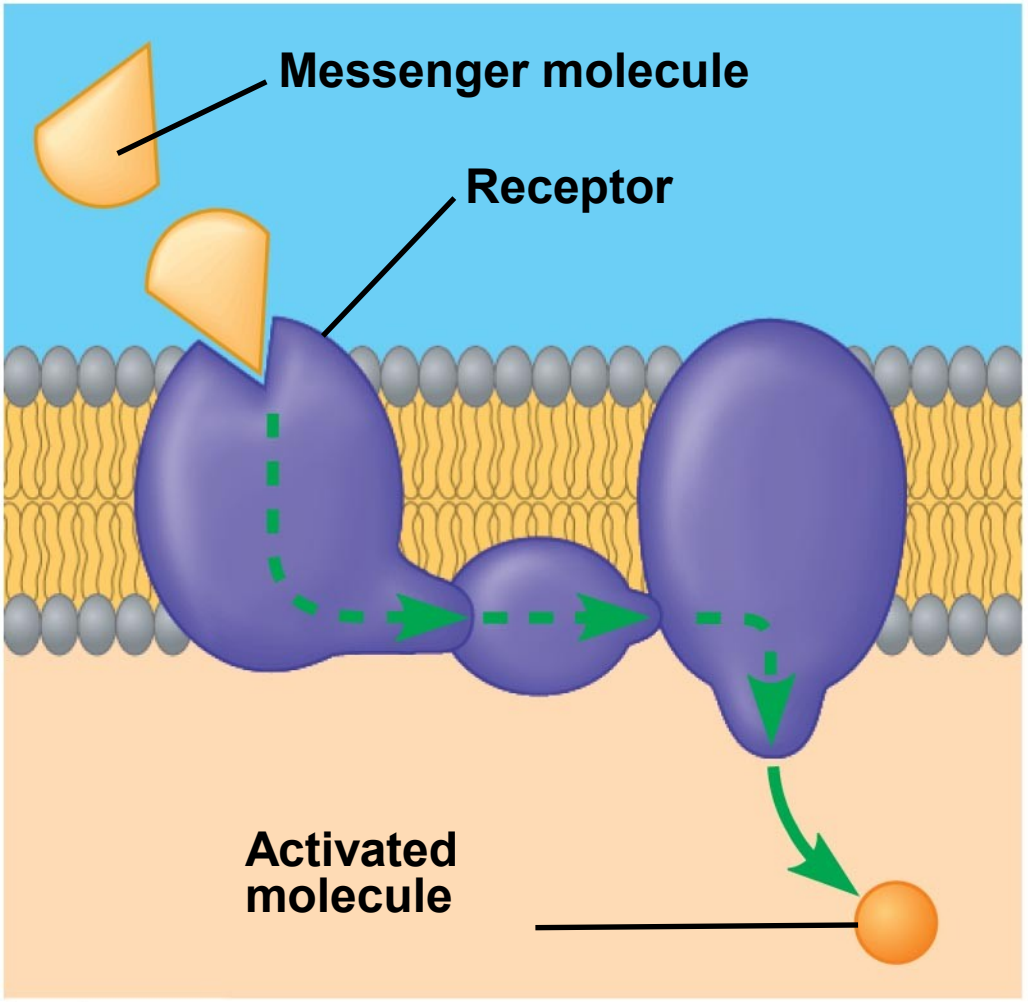
- Signal transduction (receptor) proteins bind hormones and other substances on the outside of the cell.
  - Binding triggers a change inside the cell.
    - *Called signal transduction*
    - Example: The binding of insulin to insulin receptors causes the cell to put glucose transport proteins into the membrane.

Fig. 5-1c



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Transport Proteins

- **Passive Transport Proteins**
  - allow water soluble substances (small polar molecules and ions) to pass through the membrane without any energy cost
- **Active Transport Proteins**
  - The cell expends energy to transport water soluble substances *against* their concentration gradient

Transport of Substances Across the Plasma Membrane (PM)

1. Passive Transport
   - (Simple) Diffusion (5.3)
   - Facilitated diffusion (5.6)
   - Osmosis (5.4, 5.5)
1. Active Transport (5.8)
2. Bulk Flow (5.9)
   - Endocytosis
   - Exocytosis

Passive Transport

- **In passive transport substances cross the membrane by diffusion**
  - Diffusion - net movement of substances from an area of high concentration to low concentration
    - no energy required

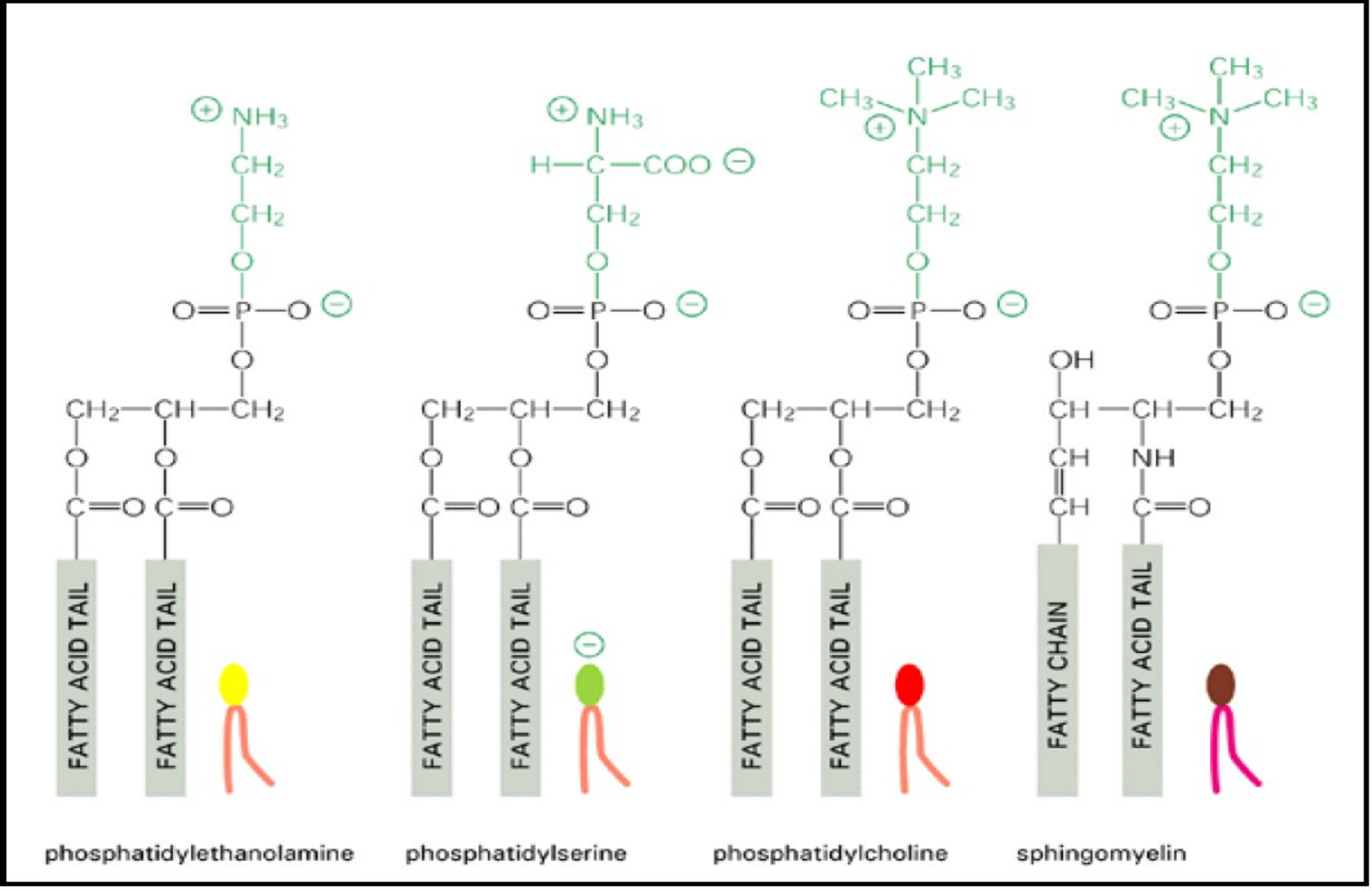


Figure 10-10. Four major phospholipids in mammalian plasma membranes. Note that different head groups are represented by different symbols in this figure and the next. All of the lipid molecules shown are derived from glycerol except for sphingomyelin, which is derived from serine

Blood group antigens

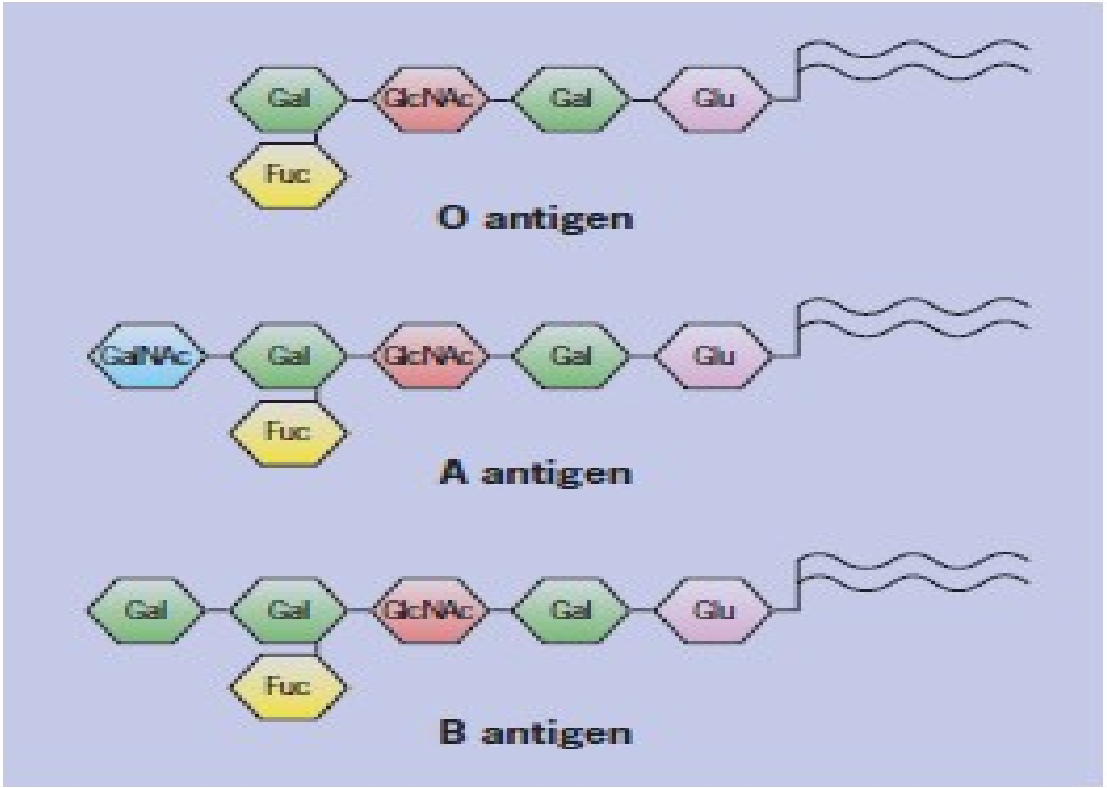
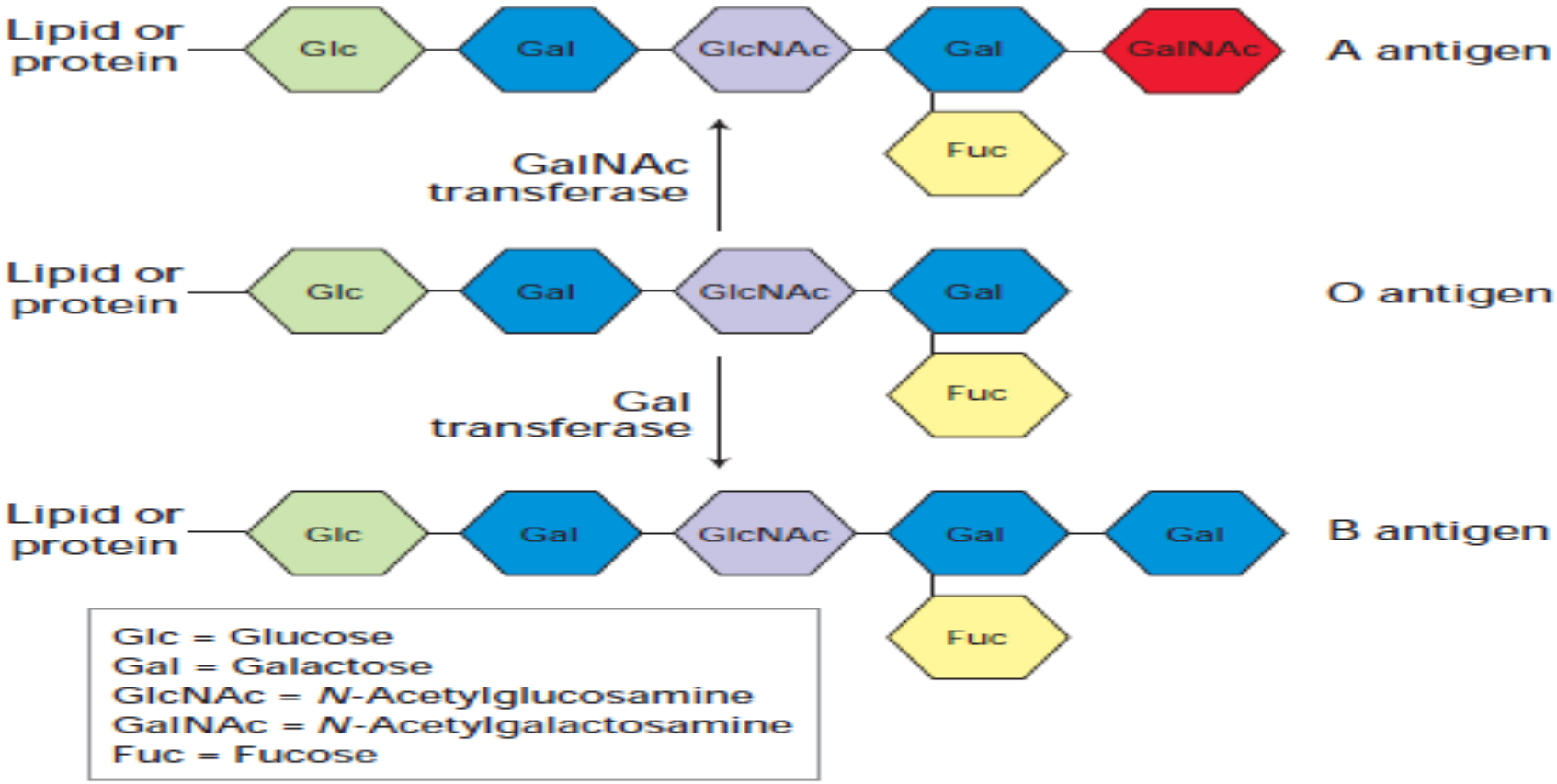


FIGURE 4.12 Blood-group antigens. Whether a person has type A, B, AB, or O blood is determined by a short chain of sugars covalently attached to membrane lipids and proteins of the red blood cell membrane. The oligosaccharides attached to membrane lipids (forming a ganglioside) that produce the A, B, and O blood types are shown here. A person with type AB blood has gangliosides with both the A and B structure. (Gal, galactose; GlcNAc, *N*-acetylglucosamine; Glu, glucose; Fuc, fucose; GalNAc, *N*-acetylgalactosamine.)



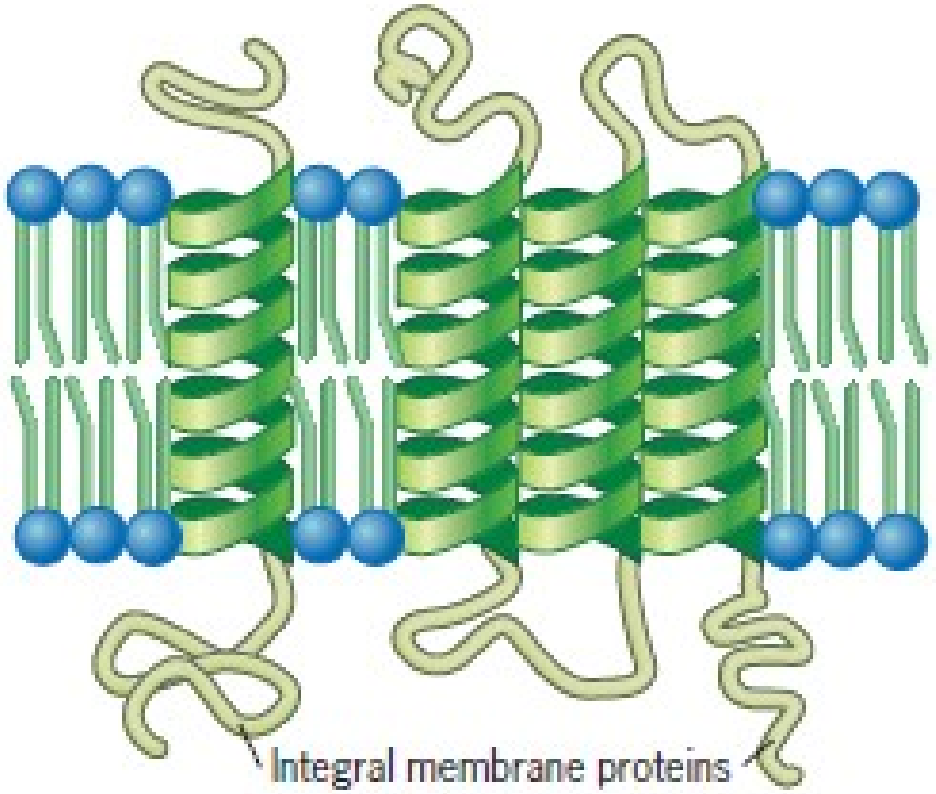
▲ **FIGURE 5-16 Human ABO blood-group antigens.** These antigens are oligosaccharide chains covalently attached to glycolipids or glycoproteins in the plasma membrane. The terminal oligosaccharide sugars distinguish the three antigens. The presence or absence of the glycosyltransferases that add galactose (Gal) or *N*-acetylgalactosamine (GalNAc) to O antigen determine a person's blood type.

TABLE 5-2 ABO Blood Groups

Blood-Group Type	Antigens on RBCs*	Serum Antibodies	Can Receive Blood Types
A	A	Anti-A	A and O
B	B	Anti-B	B and O
AB	A and B	None	All
O	O	Anti-A and anti-B	O

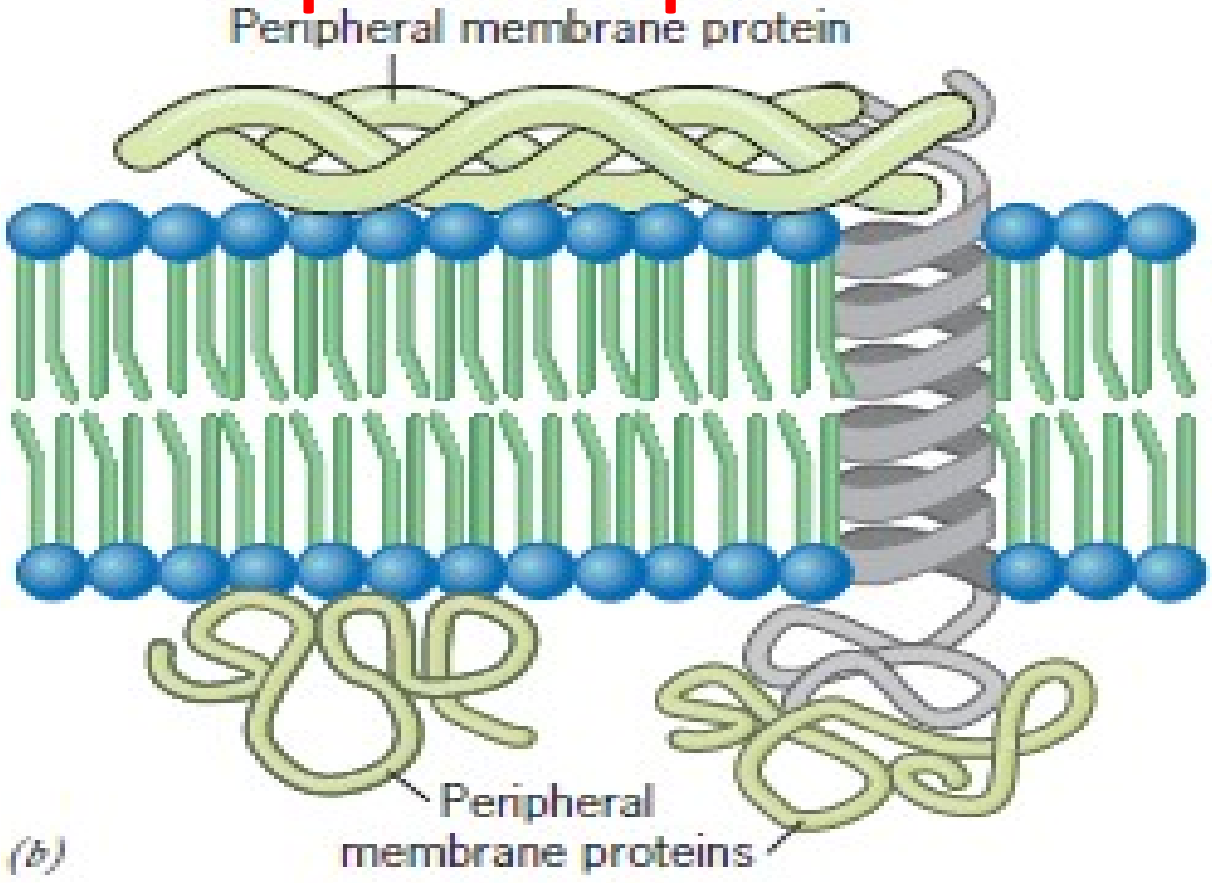
*See Figure 5-16 for antigen structures.

INTEGRAL MEMBRANE PROTEINS



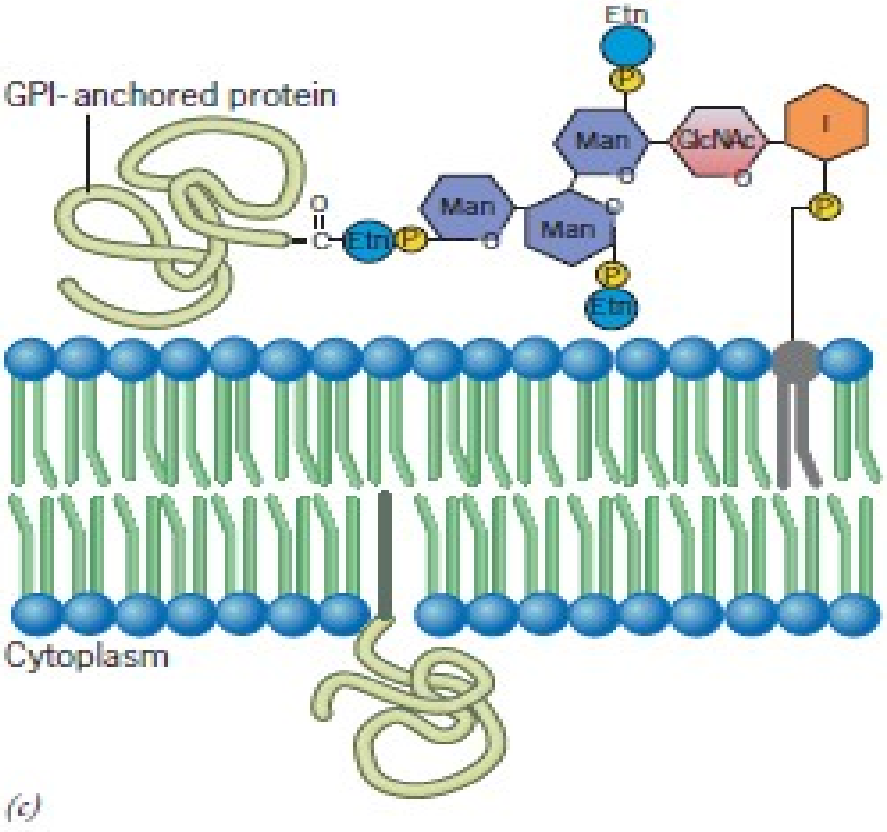
Integral membrane proteins typically contains one or more transmembrane helices

Peripheral proteins



Peripheral proteins are non covalently bonded to the polar head groups of the lipid bilayer

Lipid anchored proteins



Lipid –anchored proteins are covalently bonded to a lipid group

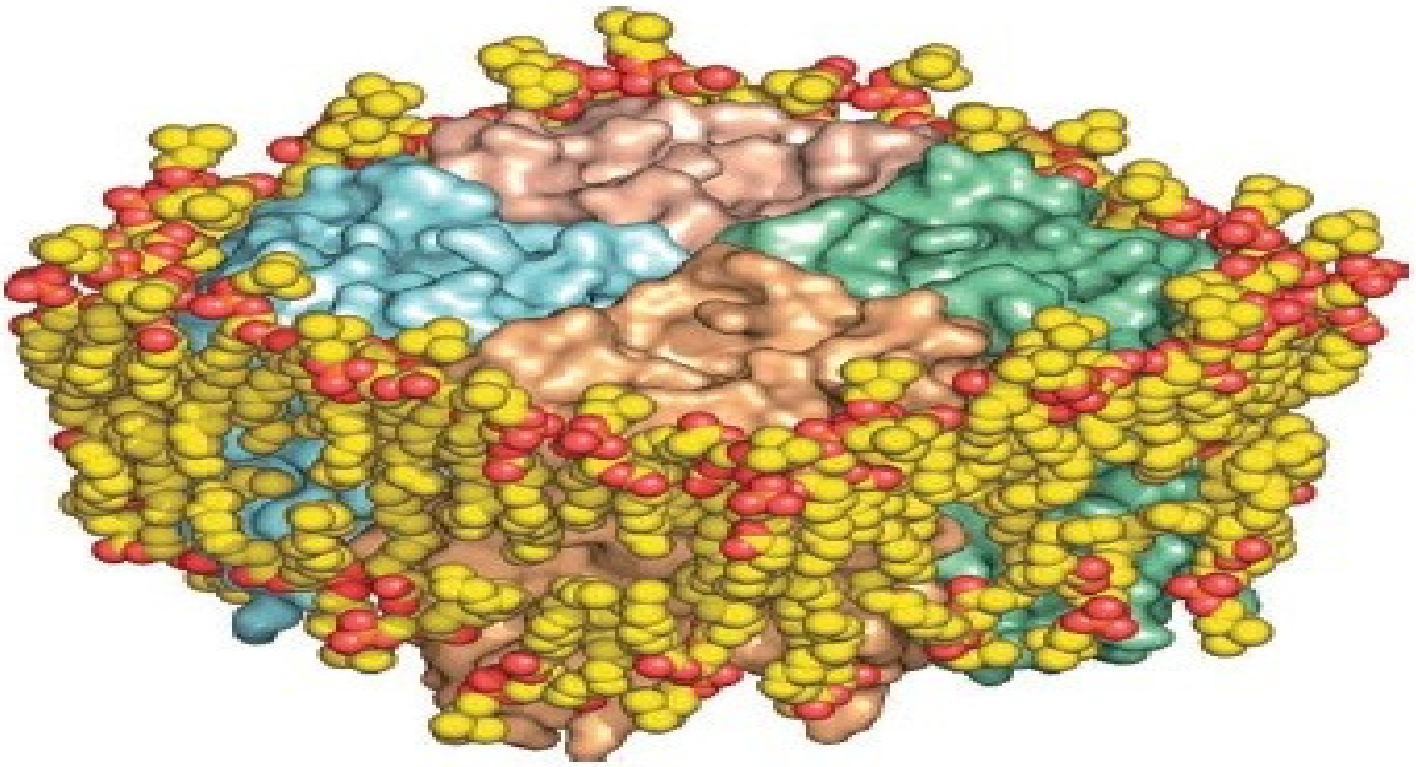
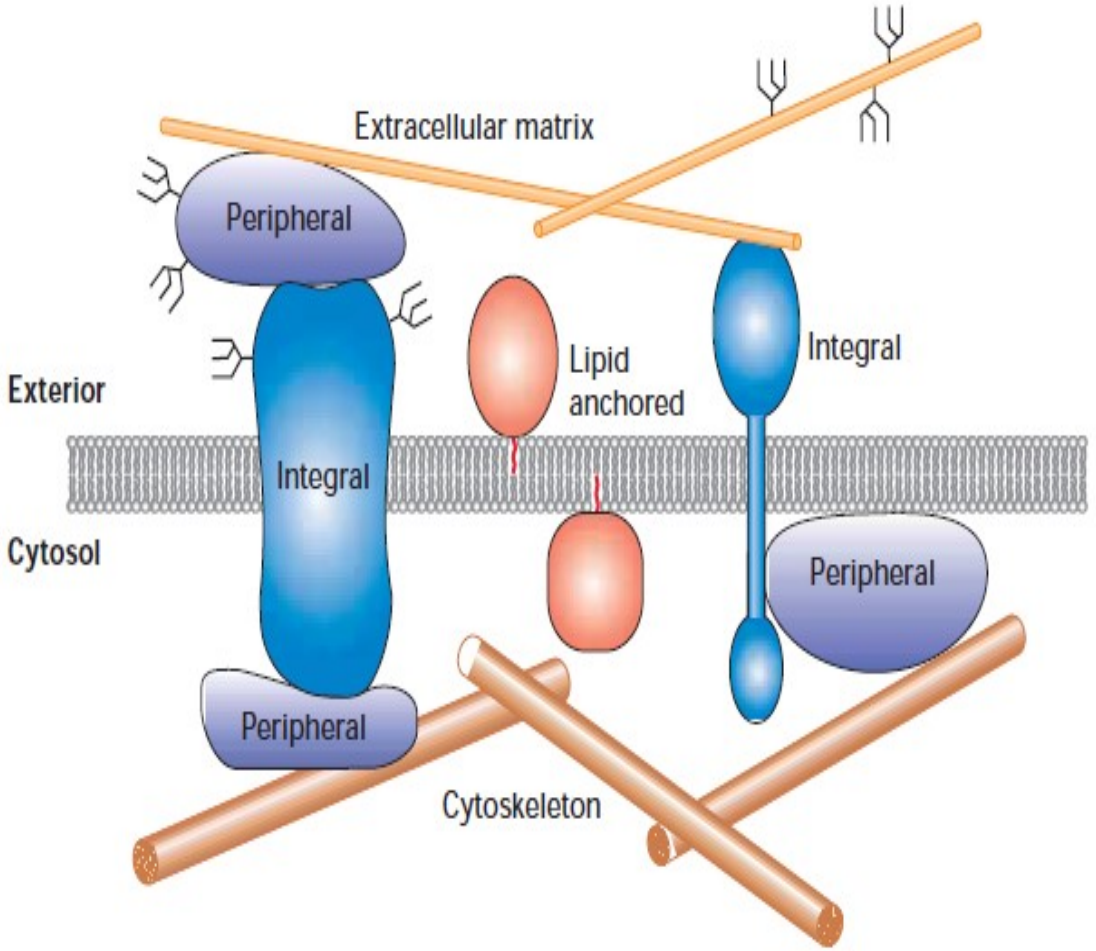


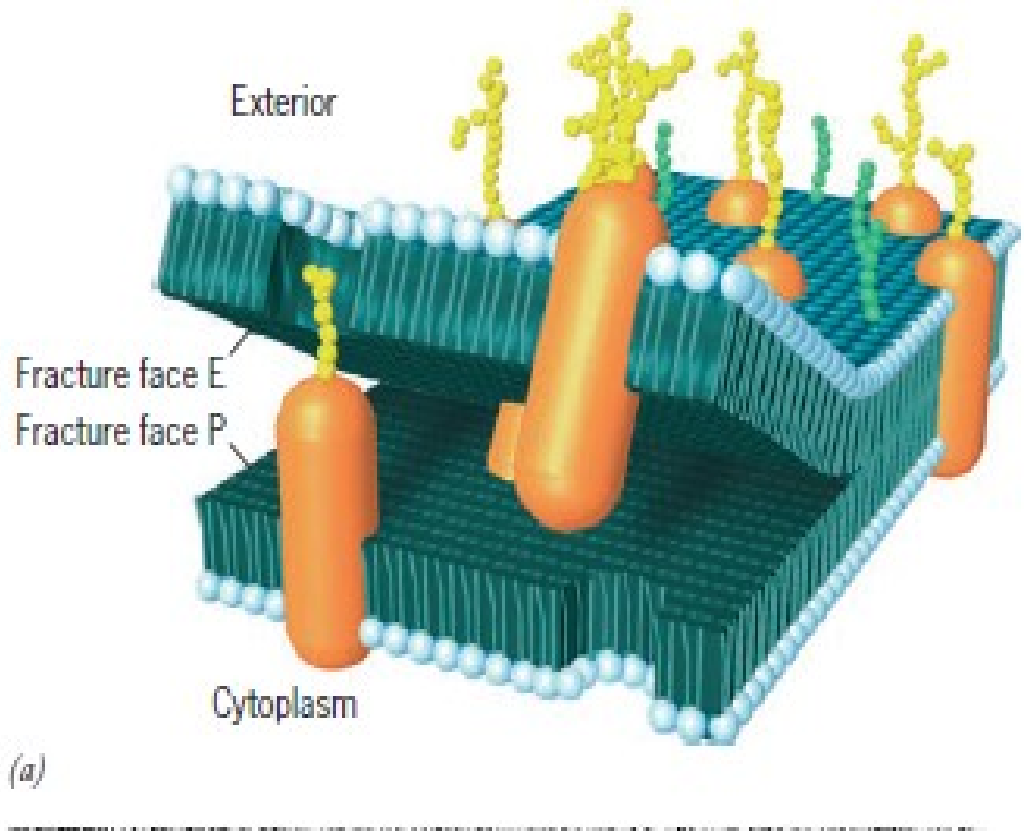
FIGURE 4.14 Proteins can be surrounded by a closely applied shell of lipid molecules. Aquaporin is a membrane protein containing four subunits (colored differently in the illustration) surrounding an aqueous channel. Analysis of the protein's structure revealed the presence of a surrounding layer of bound lipid molecules. Whether or not these lipid molecules affect the function of the aquaporin molecule is unclear, but it is likely that they are held in close proximity to the protein and thus unable to move freely within the bilayer. (FROM CAROLA HUNTE AND SEBASTIAN RICHERS, CURR. OPIN. STRUCT. BIOL. 18:407, 2008, COPYRIGHT 2008, WITH PERMISSION FROM ELSEVIER SCIENCE.)

Various classes of proteins are associated with the lipid bilayer

▶ **FIGURE 5-11 Diagram of how various classes of proteins associate with the lipid bilayer.** Integral (transmembrane) proteins span the bilayer. Lipid-anchored proteins are tethered to one leaflet by a long covalently attached hydrocarbon chain. Peripheral proteins associate with the membrane primarily by specific noncovalent interactions with integral proteins or membrane lipids. Farther from the membrane are membrane-associated proteins including the cytoskeleton, extracellular matrix in animal cells, and cell wall in plant and bacterial cells (not depicted). Carbohydrate chains are attached to many extracellular proteins and to the exoplasmic domains of many transmembrane proteins.



Freeze fracture : A technique for investigating the cell membrane structure



Freeze- fracture technique

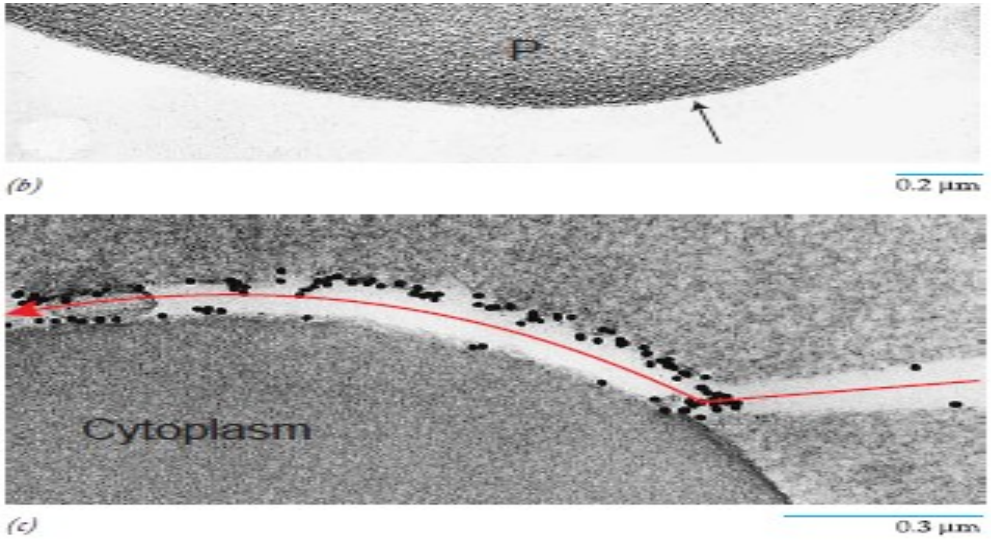


FIGURE 4.15 Freeze fracture: a technique for investigating cell membrane structure. (*a*) When a block of frozen tissue is struck by a knife blade, a fracture plane runs through the tissue, often following a path that leads it through the middle of the lipid bilayer. The fracture plane goes around the proteins rather than cracking them in half, and they segregate with one of the two halves of the bilayer. The exposed faces within the center of the bilayer can then be covered with a metal deposit to form a metallic replica. These exposed faces are referred to as the E, or ectoplasmic face, and the P, or protoplasmic face. (*b*) Replica of a freeze-fractured human erythrocyte. The P fracture face is seen to be covered with particles approximately 8 nm in diameter. A small ridge (arrow) marks the junction of the particulate face with the surrounding ice. (*c*) This micrograph shows the surface of an erythrocyte that was frozen and then fractured, but rather than preparing a replica, the cell was thawed, fixed, and labeled with a marker for the carbohydrate groups that project from the external surface of the integral protein glycophorin (Figure 4.18). Thin sections of the labeled, fractured cell reveal that glycophorin molecules (black particles) have preferentially segregated with the outer half of the membrane. The red line shows the path of the fracture plane. (B: FROM THOMAS W. TILLACK AND VINCENT T. MARCHESI, J. CELL BIOL. 45:649, 1970; C: FROM PEDRO PINTO DA SILVA AND MARIA R. TORRISI, J. CELL BIOL. 93:467, 1982; B,C: BY COPYRIGHT PERMISSION OF THE ROCKEFELLER UNIVERSITY PRESS.)

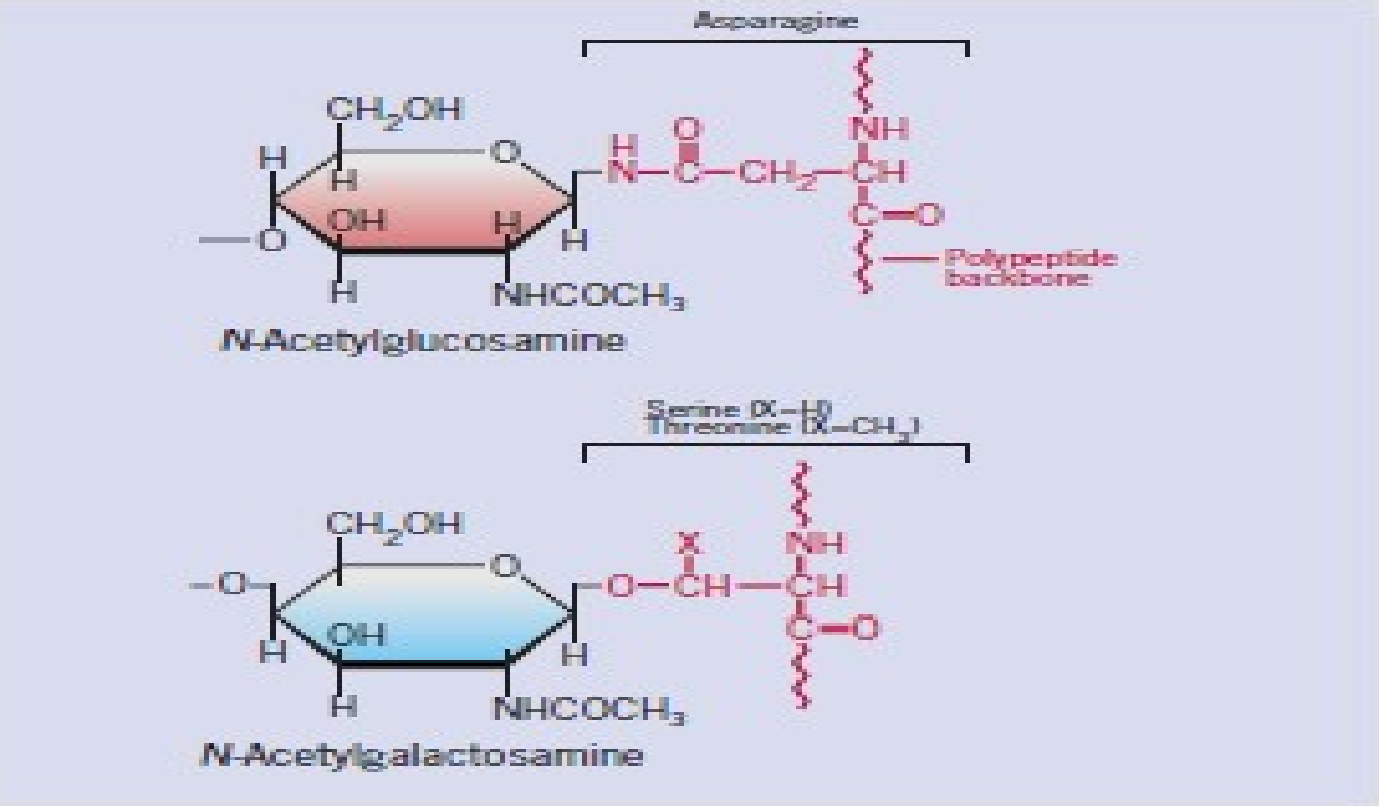


FIGURE 4.11 Two types of linkages that join sugars to a polypeptide chain. The *N*-glycosidic linkage between asparagine and *N*-acetylglucosamine is more common than the *O*-glycosidic linkage between serine or threonine and *N*-acetylgalactosamine.

Integral proteins resides in the plasma membrane

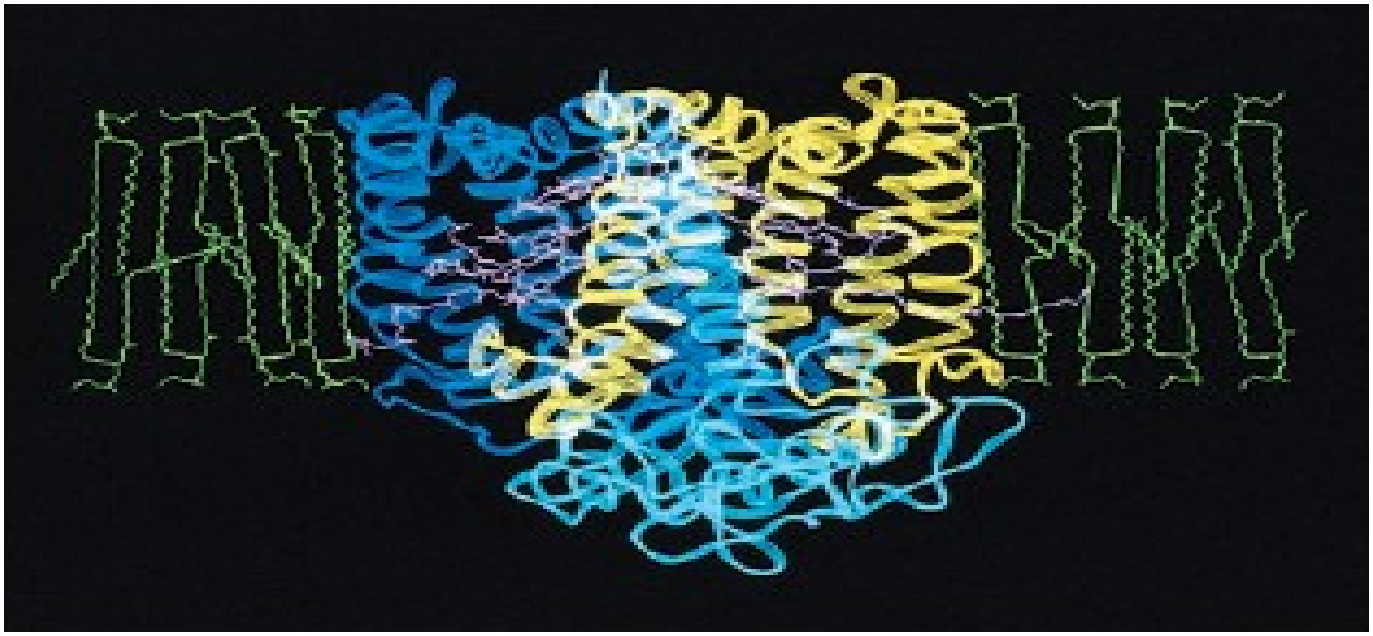


FIGURE 4.17 An integral protein as it resides within the plasma membrane. Tertiary structure of the photosynthetic reaction center of a bacterium as determined by X-ray crystallography. The protein contains three different membrane-spanning polypeptides, shown in yellow, light blue, and dark blue. The helical nature of each of the transmembrane segments is evident. (FROM G. FEHER, J. P. ALLEN, M. Y. OKAMURA, AND D. C. REES, REPRINTED WITH PERMISSION FROM NATURE 339:113, 1989; COPYRIGHT 1989, MACMILLAN MAGAZINES LIMITED.)

Glycoporin a integral protein with a single transmembrane domain

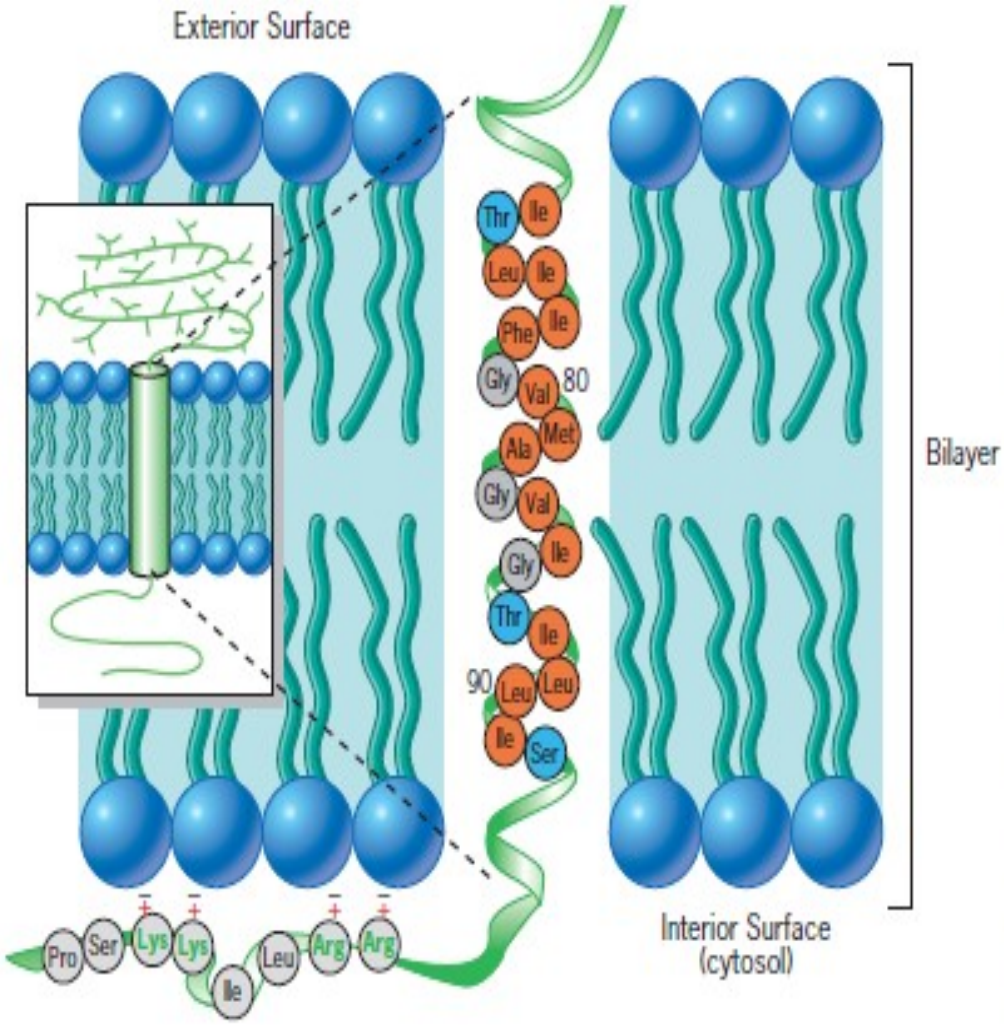


FIGURE 4.18 Glycophorin A, an integral protein with a single transmembrane domain. The single α helix that passes through the membrane consists predominantly of hydrophobic residues (orange-colored circles). The four positively charged amino acid residues of the cytoplasmic domain of the membrane form ionic bonds with negatively charged lipid head groups. Carbohydrates are attached to a number of amino acid residues on the outer surface of the protein (shown in the inset). All but one of the 16 oligosaccharides are small *O*-linked chains (the exception is a larger oligosaccharide linked to the asparagine residue at position 26). Glycophorin molecules are present as homodimers within the erythrocyte membrane (Figure 4.32*d*). The two helices cross over one another in the region between residues 79 and 83. This Gly-X-X-X-Gly sequence is commonly found where transmembrane helices come into close proximity.

Various amino acid residues within trans membrane helices

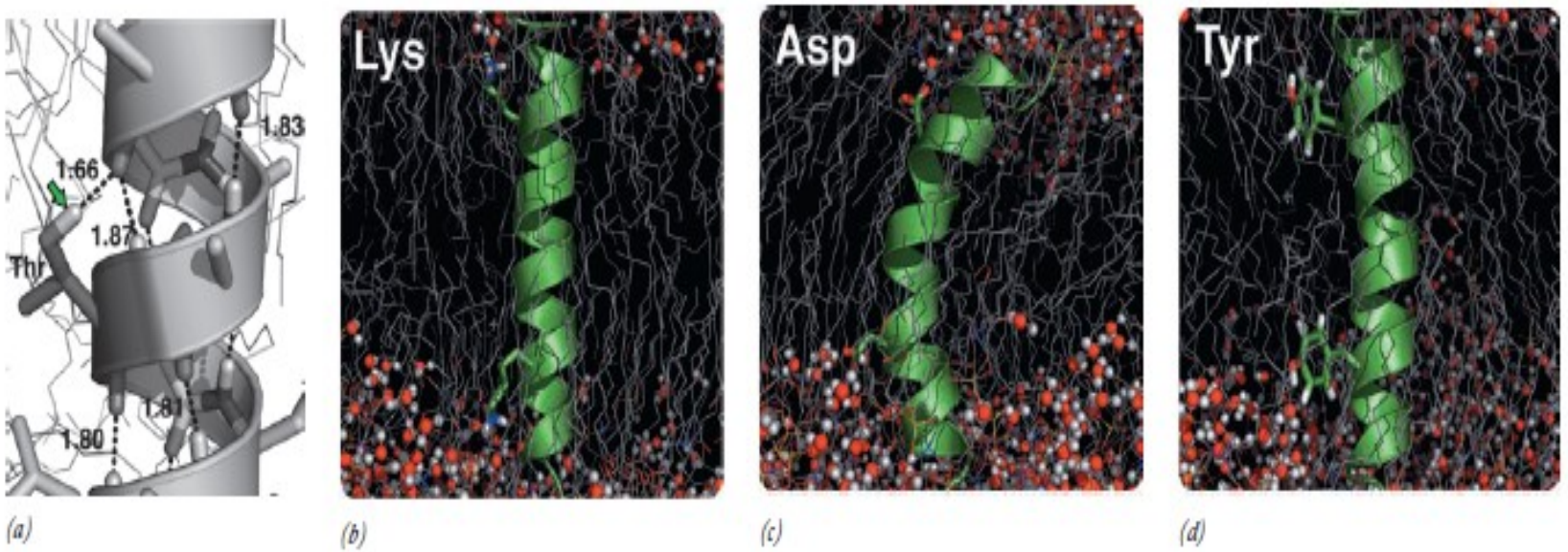
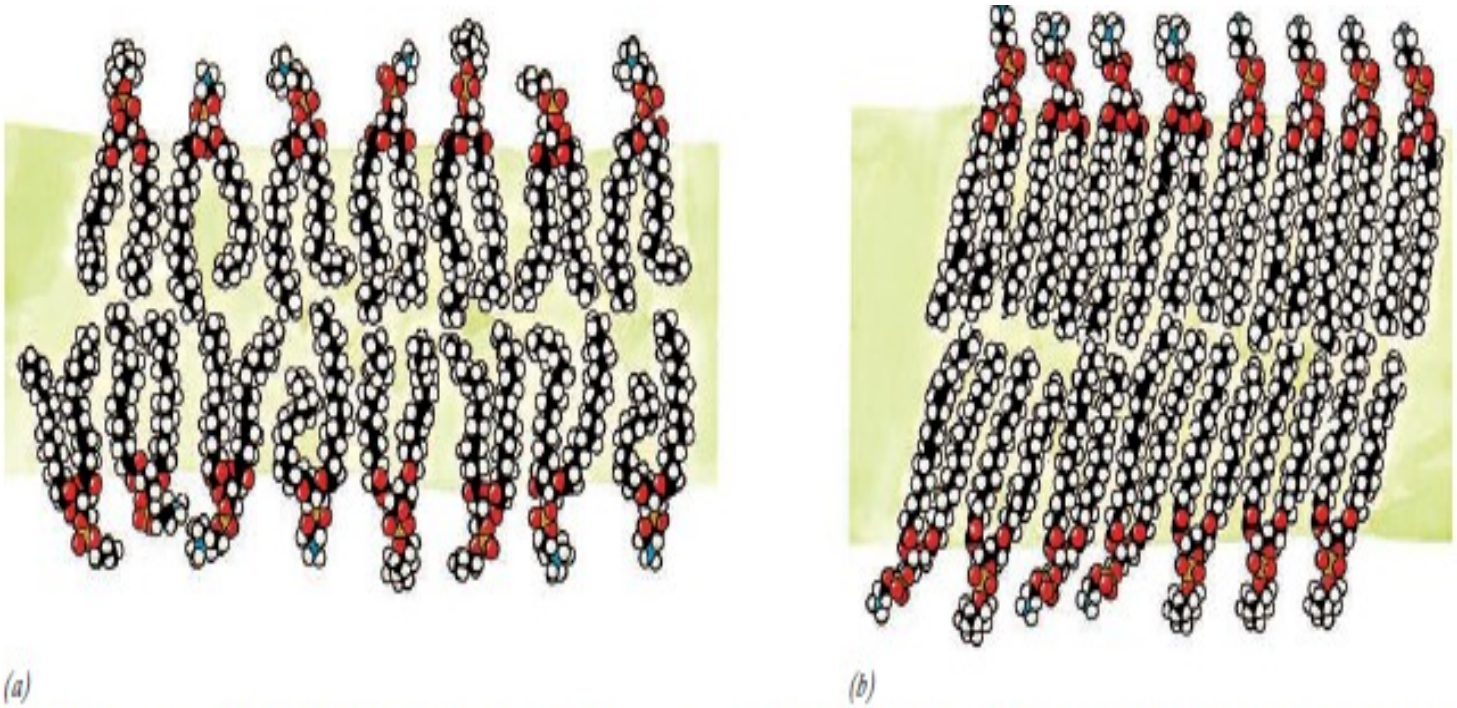


FIGURE 4.19 Accommodating various amino acid residues within transmembrane helices. (*a*) In this portrait of a small portion of a transmembrane helix, the hydroxyl group of the threonine side chain (arrow) is able to form a (shared) hydrogen bond with a backbone oxygen within the lipid bilayer. Hydrogen bonds are indicated by the dashed lines and their distances are shown in angstroms. (*b*) The side chains of the two lysine residues of this transmembrane helix are sufficiently long and flexible to form bonds with the head groups and water molecules of the polar face of the lipid bilayer. (*c*) The side chains of the two aspartic acid residues of this transmembrane helix can also reach the polar face of the bilayer but introduce distortion in the helix to do so. (*d*) The aromatic side chains of the two tyrosine residues of this transmembrane helix are oriented perpendicular to the axis of the membrane and parallel to the fatty acyl chains with which they interact. (FROM ANNA C. V. JOHANSSON AND ERIK LINDAHL, BIOPHYS. J. 91:4459, 4453, 2006.)

Transition temparature

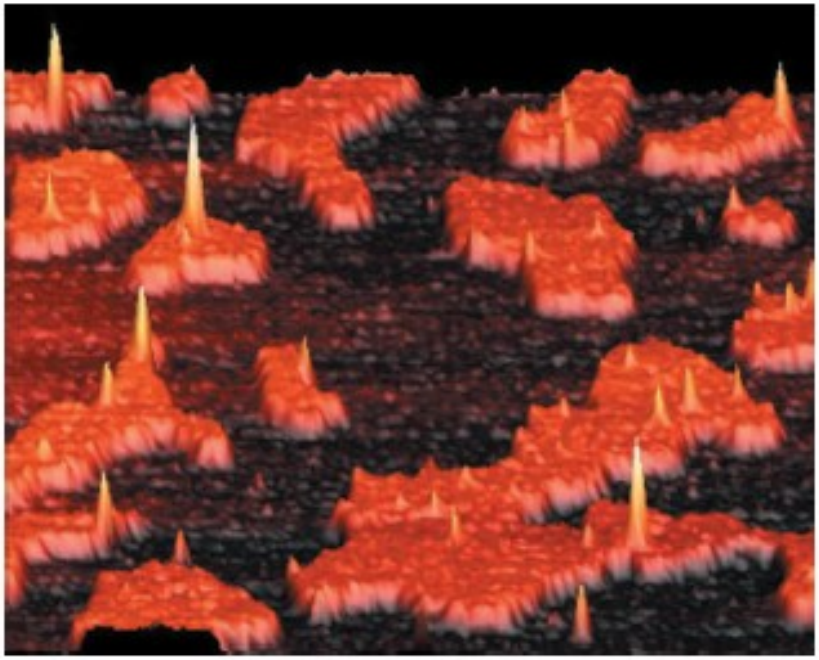


(a) (b)

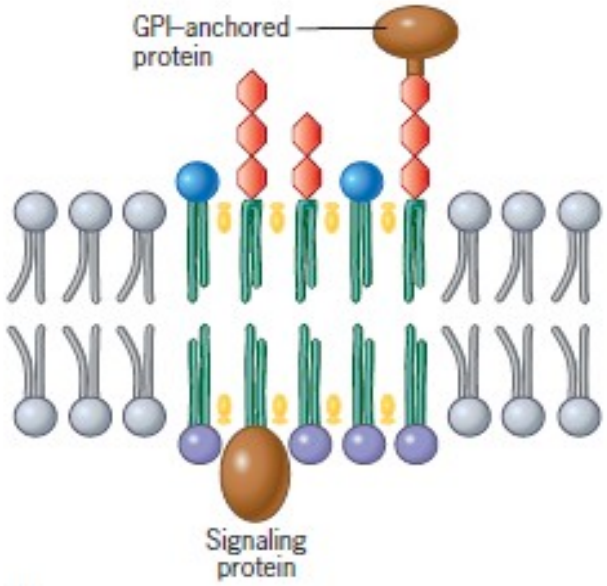
FIGURE 4.23 The structure of the lipid bilayer depends on the temperature. The bilayer shown here is composed of two phospholipids: phosphatidylcholine and phosphatidylethanolamine. (*a*) Above the transition temperature, the lipid molecules and their hydrophobic tails are free to move in certain directions, even though they retain a considerable degree of order. (*b*) Below the transition temperature, the movement of the molecules is greatly restricted, and the entire bilayer can be described as a crystalline gel. (AFTER R. N. ROBERTSON, THE LIVELY MEMBRANES, CAMBRIDGE UNIVERSITY PRESS; 1983, REPRINTED WITH PERMISSION OF CAMBRIDGE UNIVERSITY PRESS.)

LIPID RAFTS – GPI ANCHORED PROTEINS

ordered regions of the bilayer (Figure 4.24*a*).



(*a*)



(*b*)

FIGURE 4.24 Lipid rafts. (*a*) Image of the upper surface of an artificial lipid bilayer containing phosphatidylcholine, which appears as the black background, and sphingomyelin molecules, which organize themselves spontaneously into the orange-colored rafts. The yellow peaks show the positions of a GPI-anchored protein, which is almost exclusively raft-associated. This image is provided by an atomic force microscope, which measures the height of various parts of the specimen at the molecular level. (*b*) Schematic model of a lipid raft within a cell. The outer leaflet of the raft consists primarily of cholesterol (yellow) and sphingolipids (red head groups). Phosphatidylcholine molecules (blue head groups) with long saturated fatty acids also tend to concentrate in this region. GPI-anchored proteins are thought to become concentrated in lipid rafts. The lipids in the outer leaflet of the raft have an organizing effect on the lipids of the inner leaflet. As a result, the inner-leaflet raft lipids consist primarily of cholesterol and glycerophospholipids with long saturated fatty acyl tails. The inner leaflet tends to concentrate lipid-anchored proteins, such as Src kinase, that are involved in cell signaling. (The controversy over the existence of lipid rafts is discussed in *Nature Cell Biol.* 9:7, 2007.) (A: FROM D. E. SASLOWSKY, ET AL., J. BIOL. CHEM. 277, COVER OF #30, 2002; COURTESY OF J. MICHAEL EDWARDSON.)

The possible movements of phospholipids in a membrane

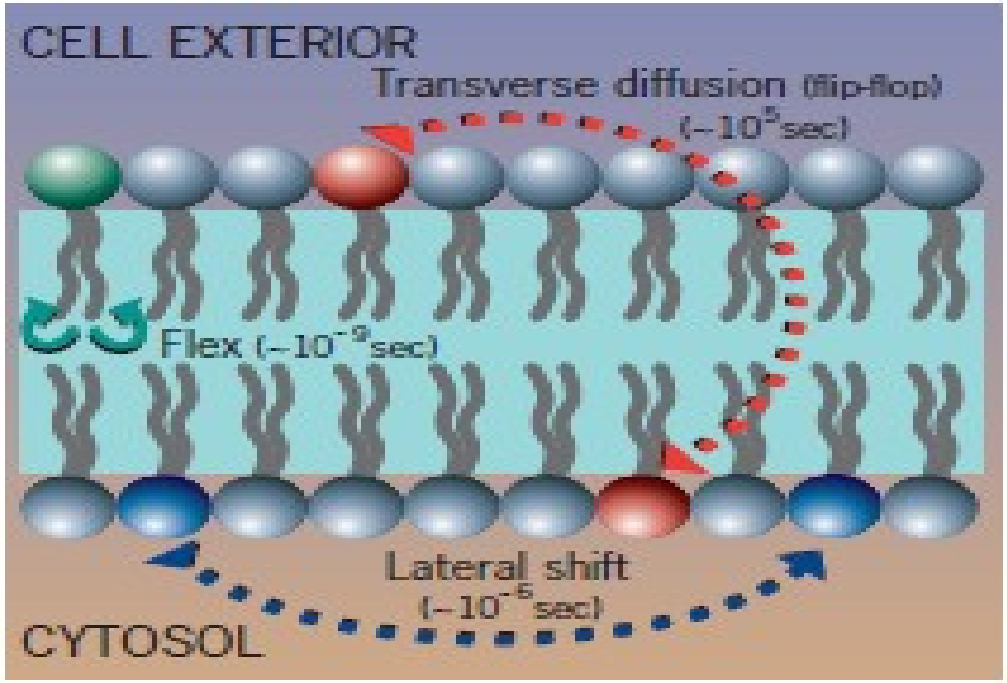


FIGURE 4.25 The possible movements of phospholipids in a membrane. The types of movements in which membrane phospholipids can engage and the approximate time scales over which they occur. Whereas phospholipids move from one leaflet to another at a very slow rate, they diffuse laterally within a leaflet rapidly. Lipids lacking polar groups, such as cholesterol, can move across the bilayer quite rapidly.

PATTERN OF MOVEMENT OF INTEGRAL PROTEINS

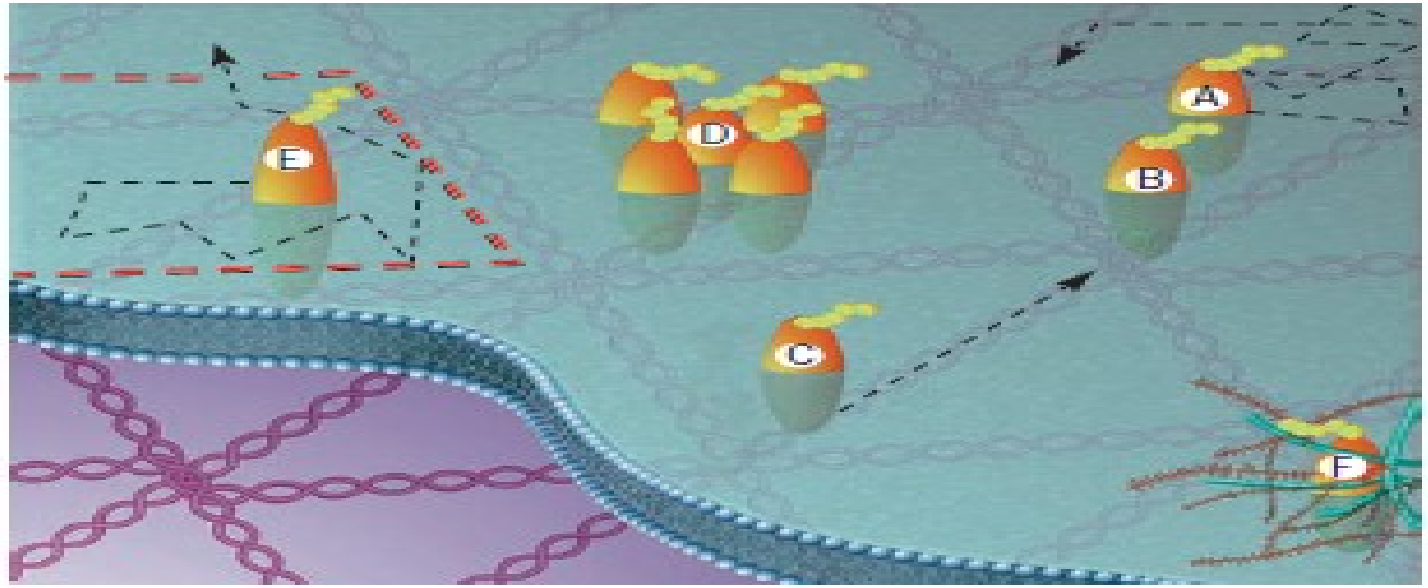


FIGURE 4.28 Patterns of movement of integral membrane proteins. Depending on the cell type and the conditions, integral membrane proteins can exhibit several different types of mobility. Protein A is capable of diffusing randomly throughout the membrane, though its rate of movement may be limited; protein B is immobilized as the result of its interaction with the underlying membrane skeleton; protein C is being moved in a particular direction as the result of its interaction with a motor protein at the cytoplasmic surface of the membrane; movement of protein D is restricted by other integral proteins of the membrane; movement of protein E is restricted by fences formed by proteins of the membrane skeleton, but it can hop into adjacent compartments through transient openings in a fence; movement of protein F is restrained by extracellular materials.

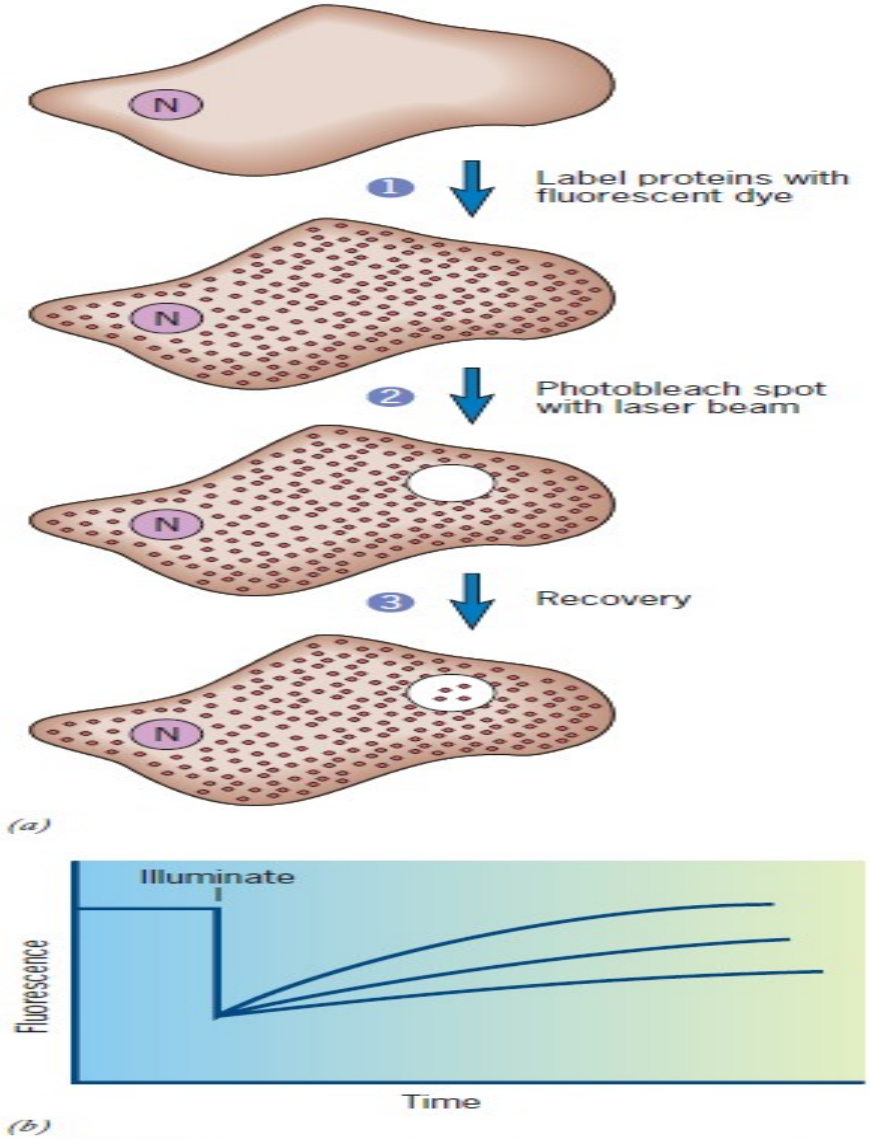


FIGURE 4.27 Measuring the diffusion rates of membrane proteins by fluorescence recovery after photobleaching (FRAP). (*a*) In this technique, a particular component of the membrane is first labeled with a fluorescent dye (step 1). A small region of the surface is then irradiated to bleach the dye molecules (step 2), and the recovery of fluorescence in the bleached region is followed over time (step 3). (N represents the cell nucleus.) (*b*) The rate of fluorescence recovery within the illuminated spot can vary depending on the protein(s) being followed. The rate of recovery is related to the diffusion coefficient of the fluorescently labeled protein.

Plasma membrane functions

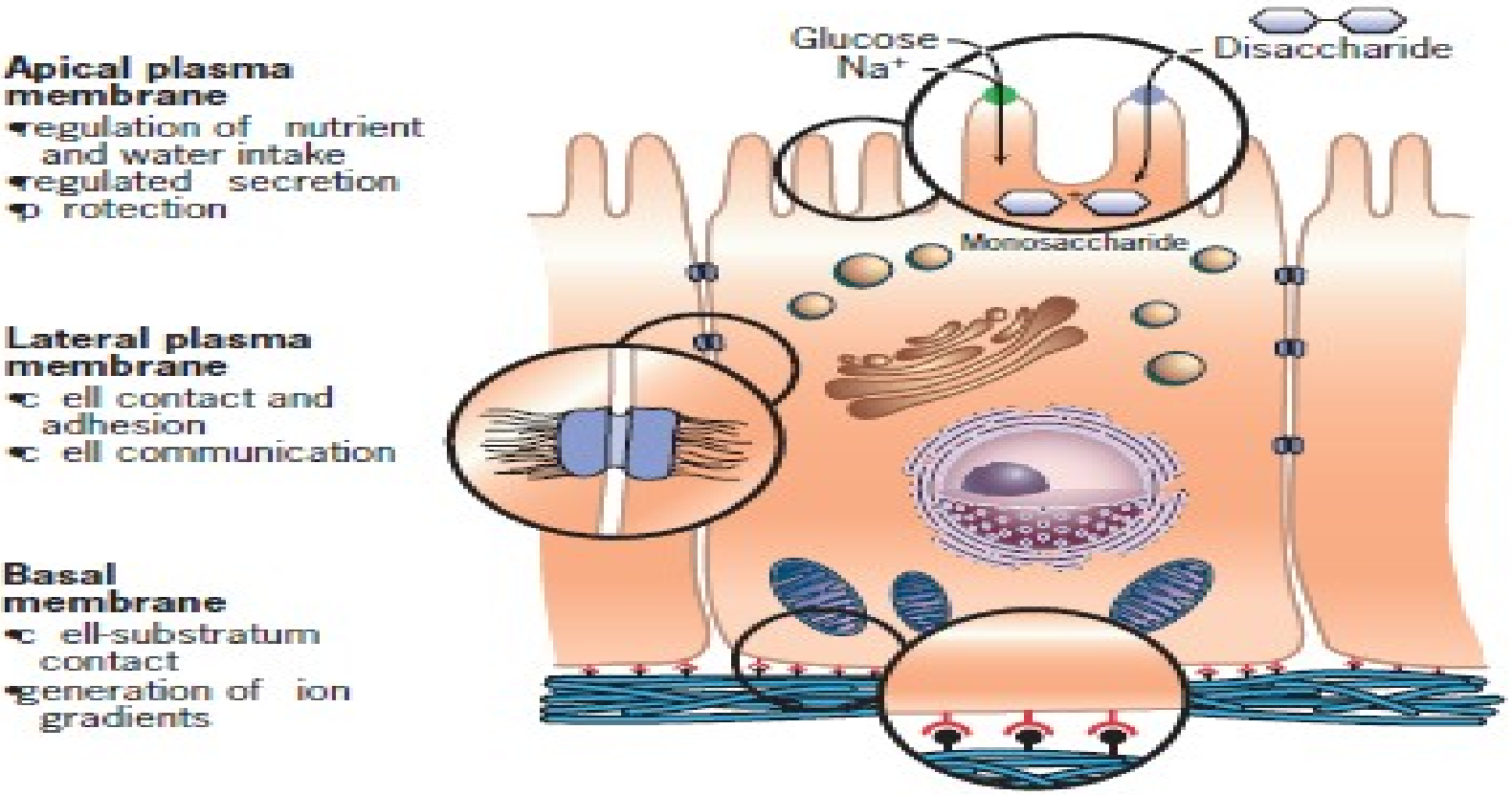
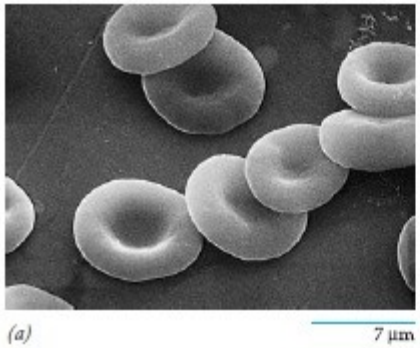
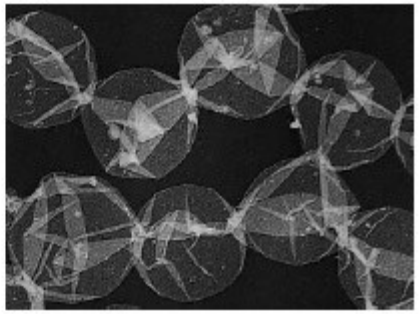


FIGURE 4.30 Differentiated functions of the plasma membrane of an epithelial cell. The apical surface of this intestinal epithelial cell contains integral proteins that function in ion transport and hydrolysis of disaccharides, such as sucrose and lactose; the lateral surface contains integral proteins that function in intercellular interaction; and the basal surface contains integral proteins that function in the association of the cell with the underlying basement membrane.

RBCS

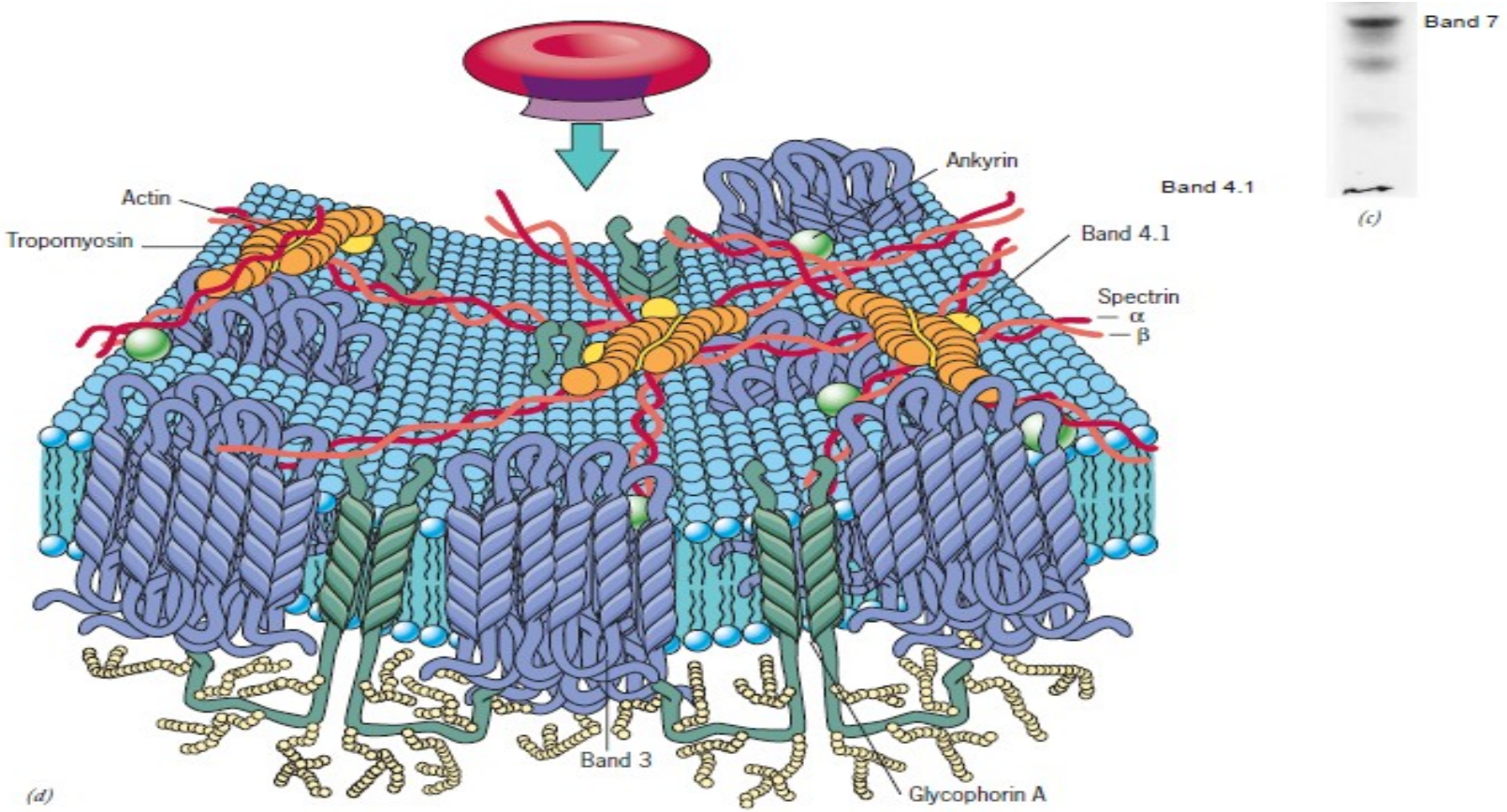


(a)



(b)

Plasma membrane of the human erythrocyte



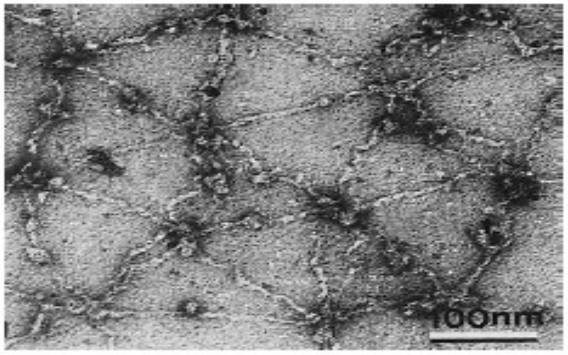
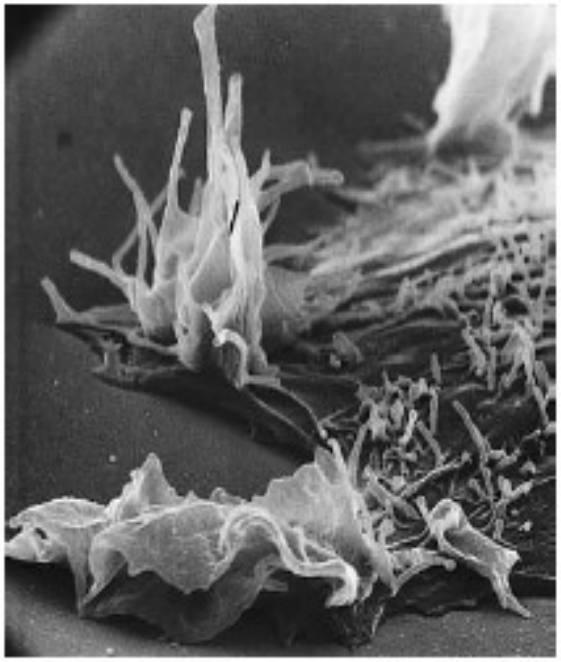
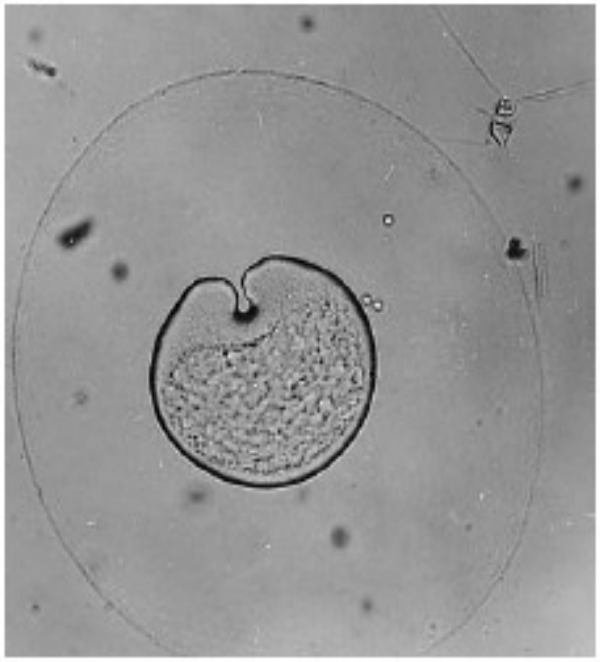


FIGURE 4.32 The plasma membrane of the human erythrocyte. (*a*) Scanning electron micrograph of human erythrocytes. (*b*) Micrograph showing plasma membrane ghosts, which were isolated by allowing erythrocytes to swell and hemolyze as described in the text. (*c*) The results of SDS–polyacrylamide gel electrophoresis (SDS–PAGE) used to fractionate the proteins of the erythrocyte membrane, which are identified at the side of the gel. (*d*) A model of the erythrocyte plasma membrane as viewed from the internal surface, showing the integral proteins embedded in the lipid bilayer and the arrangement of peripheral proteins that make up the membrane's internal skeleton. The band 3 dimer shown here is simplified. The band 4.1 protein stabilizes actin–spectrin complexes. (*e*) Electron micrograph showing the arrangement of the proteins of the inner membrane skeleton. (A: COURTESY FRANÇOIS M. M. MOREL, RICHARD F. BAKER, AND HAROLD WAYLAND, J. CELL BIOL. 48:91, 1971; B: COURTESY OF JOSEPH F. HOFFMAN; C: REPRODUCED, WITH PERMISSION, FROM V. T. MARCHESI, H. FURTHMAYR, AND M. TOMITA, ANNU. REV. BIOCHEM. VOL. 45; © 1976 BY ANNUAL REVIEWS INC.; D: AFTER D. VOET AND J. G. VOET, BIOCHEMISTRY, 2D ED.; COPYRIGHT © 1995, JOHN WILEY & SONS, INC.; E: FROM SHIH-CHUN LIU, LAURA H. DERICK, AND JIRI PALEK, J. CELL BIOL. 104:527, 1987; A, E: BY COPYRIGHT PERMISSION OF THE ROCKEFELLER UNIVERSITY PRESS.)

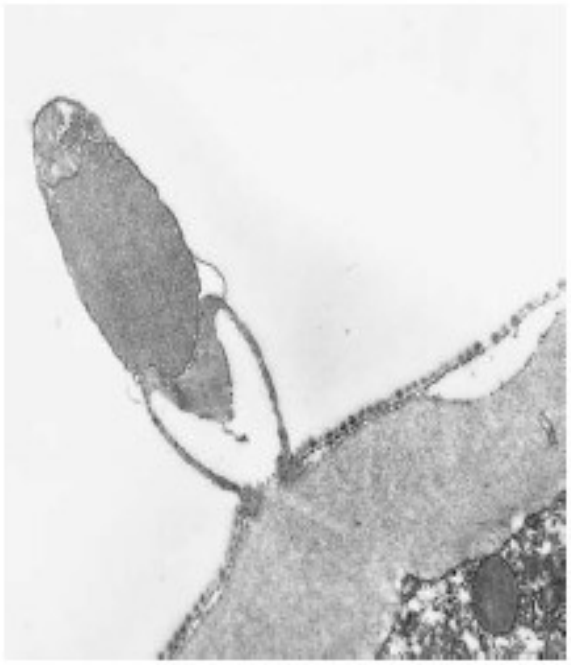
The dynamic properties of the plasma membrane



(a)



(b)



(c)

FIGURE 4.8 The dynamic properties of the plasma membrane. (*a*) The leading edge of a moving cell often contains sites where the plasma membrane displays undulating ruffles. (*b*) Division of a cell is accompanied by the deformation of the plasma membrane as it is pulled toward the center of the cell. Unlike most dividing cells, the cleavage furrow of this dividing ctenophore egg begins at one pole and moves unidirectionally through the egg. (*c*) Membranes are capable of fusing with other membranes. This sperm and egg are in a stage leading to the fusion of their plasma membranes. (A: COURTESY OF JEAN PAUL REVEL; B: COURTESY OF GARY FREEMAN; C: COURTESY OF A. L. COLWIN AND L. H. COLWIN.)