Prokaryotic Cell Structure
-Cell Envelope-

Lecture II

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The Cell Envelope

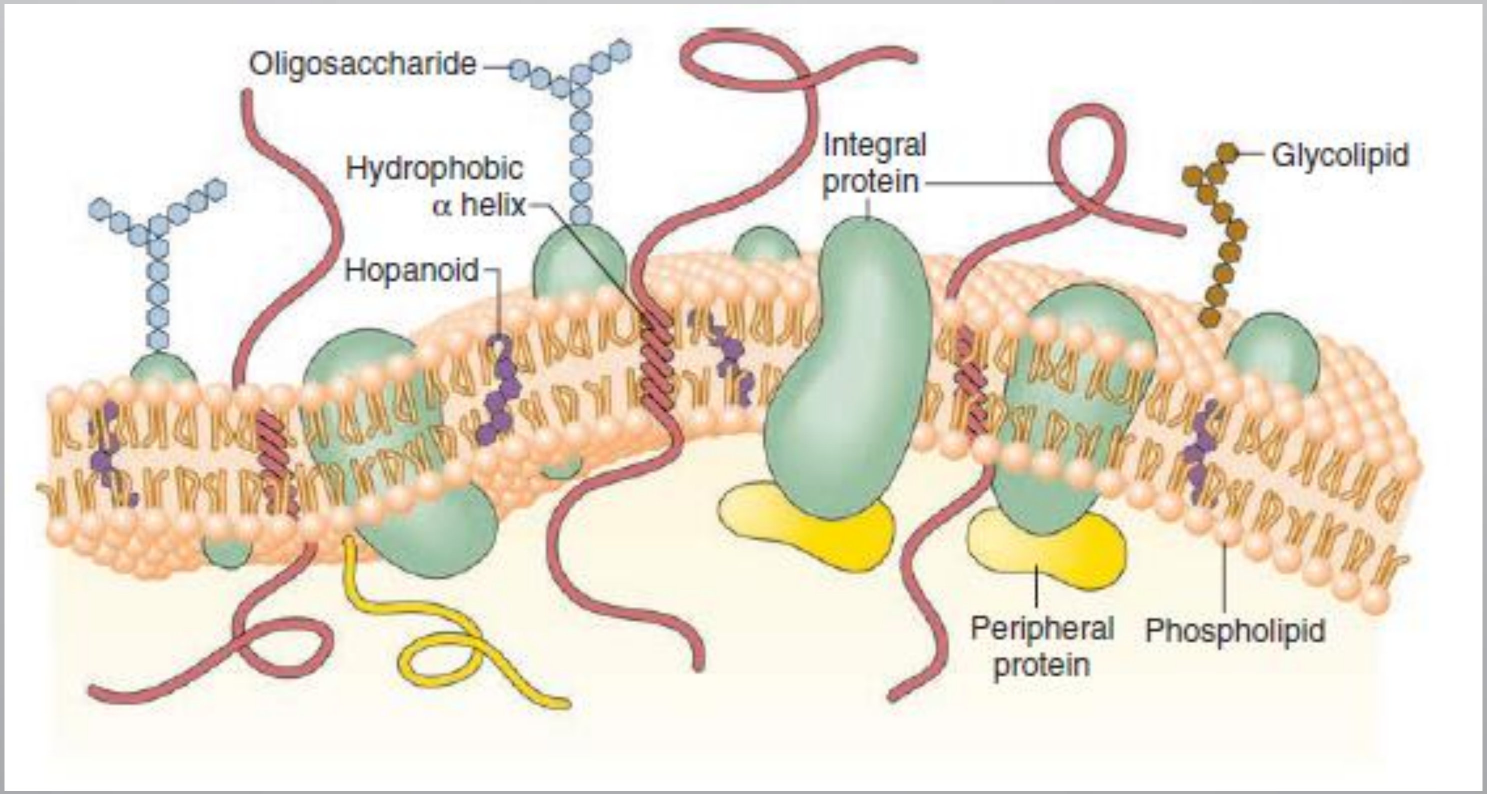
Prokaryotic cells are surrounded by complex envelope layers that differ in composition among the major groups. These structures protect the organisms from hostile environments,

such as extreme osmolarity, harsh chemicals, and even antibiotics.

The Cell Membrane

- **A. Structure**

The bacterial cell membrane, also called the cytoplasmic membrane, is visible in electron micrographs of thin sections. It is a typical “unit membrane” composed of phospholipids and upward of 200 different kinds of proteins. Proteins account for approximately 70% of the mass of the membrane, which is a considerably higher proportion than that of mammalian cell membranes.



Bacterial Plasma Membrane Structure. This diagram of the fluid mosaic model of bacterial membrane structure shown the integral proteins (green and red) floating in a lipid bilayer. Peripheral proteins (yellow) are associated loosely with the inner membrane surface. Small spheres represent the hydrophilic ends of membrane phospholipids and wiggly tails, the hydrophobic fatty acid chains. Other membrane lipids such as hopanoids (purple) may be present. For the sake of clarity, phospholipids are shown proportionately much larger size than in real membranes

The membranes of prokaryotes are distinguished from those of eukaryotic cells by the absence of sterols, the only exception being mycoplasmas that incorporate sterols, such as cholesterol, into their membranes when growing in sterol-containing media.

B. Function

The major functions of the cytoplasmic membrane are

(1) selective permeability and transport of solutes;

(2) electron transport and oxidative phosphorylation in aerobic species.

(3) excretion of hydrolytic exoenzymes.

(4) bearing the enzymes and carrier molecules that function in the biosynthesis of DNA, cell wall polymers, and membrane lipids; and

(5) bearing the receptors and other proteins of the chemotactic and other sensory transduction systems.

At least 50% of the cytoplasmic membrane must be in the semifluid state for cell growth to occur. At low temperatures, this is achieved by greatly increased synthesis and incorporation of unsaturated fatty acids into the phospholipids of the cell membrane.

The Cell Wall

The internal osmotic pressure of most bacteria ranges from 5 to 20 atm as a result of solute concentration via active transport. In most environments, this pressure would be sufficient to burst the cell were it not for the presence of a high-tensile strength cell wall. The bacterial cell wall owes its strength to a layer composed of a substance variously referred to as murein, mucopeptide, or peptidoglycan (all are synonyms). Most bacteria are classified as gram-positive or gram negative according to their response to the Gram-staining procedure. This procedure was named for the histologist Hans Christian Gram, who developed this differential staining procedure in an attempt to stain bacteria in infected tissues. The Gram stain depends on the ability of certain bacteria (the gram-positive bacteria) to retain a complex of crystal violet (a purple dye) and iodine after a brief wash with alcohol or acetone. Gram-negative bacteria do not retain the dye–iodine complex and become translucent, but they can then be counterstained with safranin (a red dye)

- **Thus, gram-positive bacteria look purple under the microscope, and gram-negative bacteria look red. The distinction between these two groups turns out to reflect fundamental differences in their cell envelopes**

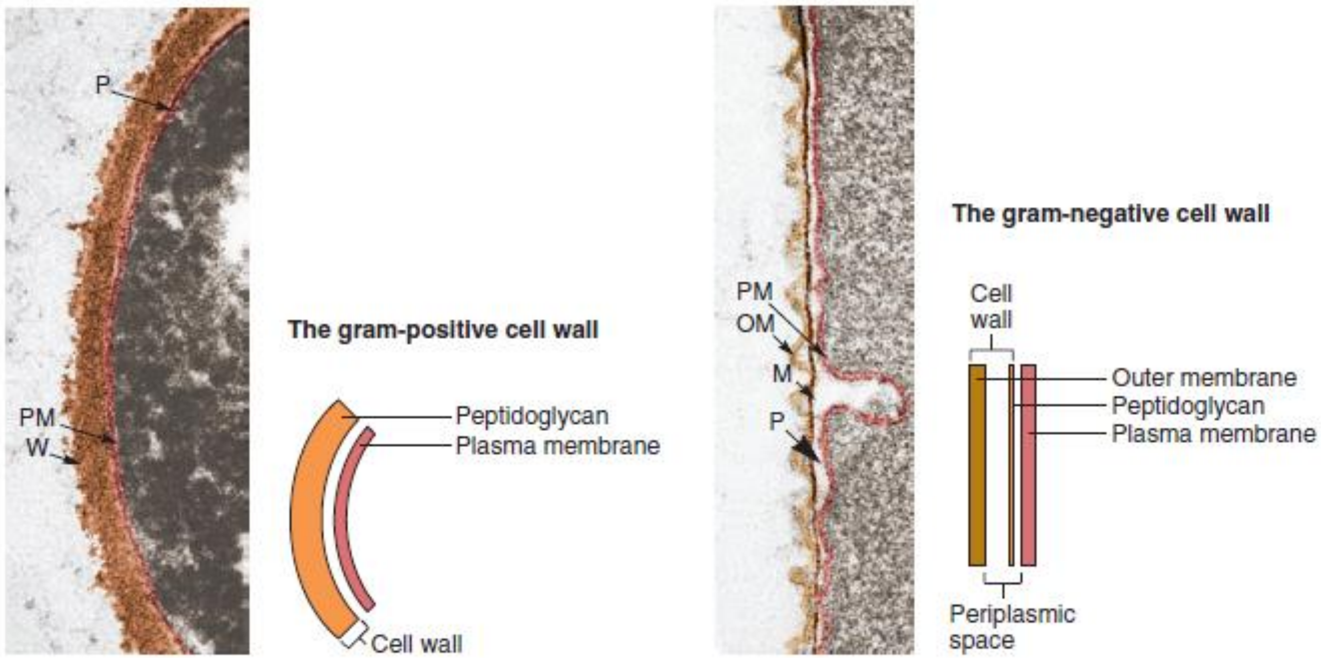


FIGURE 2-15 Gram-positive and gram-negative cell walls. The gram-positive envelope is from *Bacillus licheniiformis* (**left**), and the gram-negative micrograph is of *Aquaspirillum serpens* (**right**). IM, plasma membrane; M; peptidoglycan or murein layer; OM, outer membrane; P, periplasmic space; W, gram-positive peptidoglycan wall. (Reproduced with permission from T. J. Beveridge/Biological Photo Service.)

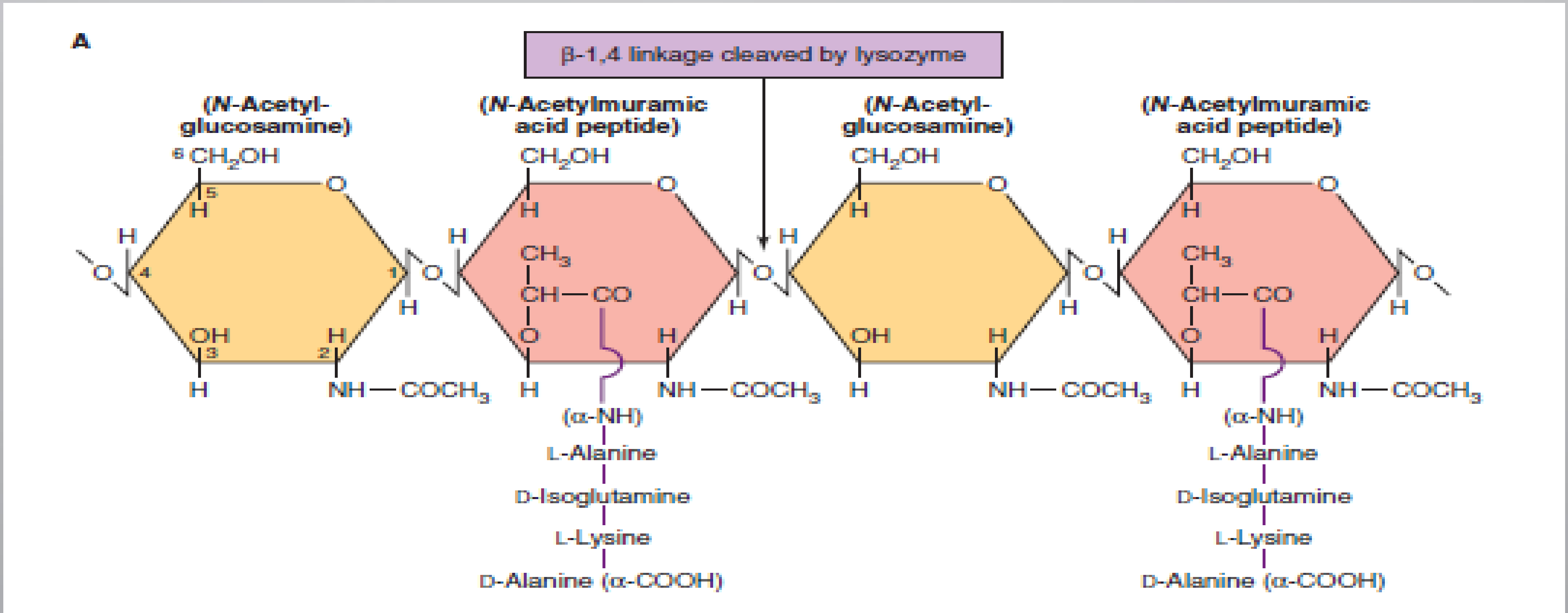
In addition to giving osmotic protection, the cell wall plays an essential role in cell division as well as serving as a primer for its own biosynthesis. Various layers of the wall are the sites of major antigenic determinants of the cell surface, and one component—the lipopolysaccharide of gram-negative cell walls—is responsible for the nonspecific endotoxin activity of gram-negative bacteria. The cell wall is, in general, non-selectively permeable; one layer of the gram-negative wall, however—the outer membrane—hinders the passage of relatively large molecules.

A. The Peptidoglycan Layer

Peptidoglycan is a complex polymer consisting, for the purposes of description, of three parts: a backbone, composed of alternating *N*-acetylglucosamine and *N*-acetylmuramic acid connected by β1→4 linkages; a set of identical tetrapeptide side chains attached to *N*-acetylmuramic acid; and a set of identical peptide cross-bridges . The backbone is the same in all bacterial species; the tetrapeptide side chains and the peptide cross-bridges vary from species to species. In many gram-negative cell walls, the cross-bridge consists of a direct peptide linkage between the diaminopimelic acid (DAP) amino group of one side chain and the carboxyl group of the terminal d-alanine of a second side chain.

Diaminopimelic acid is a unique element of bacterial cell walls. It is never found in the cell walls of *Archaea* or eukaryotes.

The fact that all peptidoglycan chains are cross-linked means that each peptidoglycan layer is a single giant molecule. In gram-positive bacteria, there are as many as 40 sheets of peptidoglycan, comprising up to 50% of the cell wall material; in gram-negative bacteria, there appears to be only one or two sheets, comprising 5–10% of the wall material. Bacteria owe their shapes, which are characteristic of particular species, to their cell wall structure.



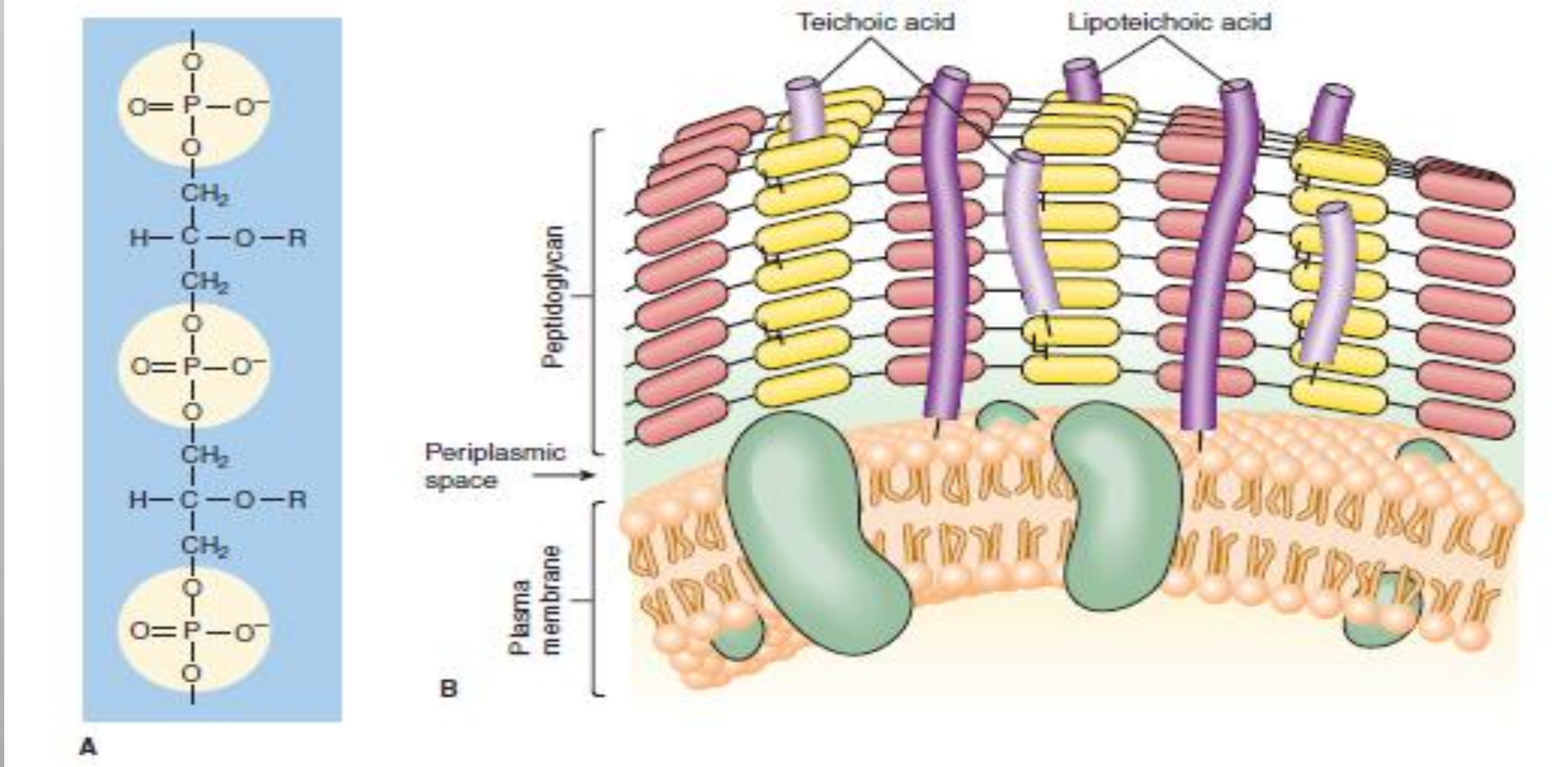
segment of the peptidoglycan of ***Staphylococcus aureus.*** **The backbone of the polymer consists of alternating subunits of *N*-acetylglucosamine and *N*-acetylmuramic acid connected by β1→4 linkages. The muramic acid residues are linked to short peptides, the composition of which varies from one bacterial species to another. In some species, the l-lysine residues are replaced by diaminopimelic acid, an amino acid that is found in nature only in prokaryotic cell walls. Note the d-amino acids, which are also characteristic constituents of prokaryotic cell walls**

- **B. Special Components of Gram-Positive Cell Walls**

Most gram-positive cell walls contain considerable amounts of **teichoic** and **teichuronic acids**, which may account for up to 50% of the dry weight of the wall and 10% of the dry weight of the total cell. In addition, some gram-positive walls may contain polysaccharide molecules.

1. Teichoic and teichuronic acids—The term *teichoic acids* encompasses all wall, membrane, or capsular polymers containing glycerophosphate or ribitol phosphate residues.

These polyalcohols are connected by phosphodiester linkages and usually have other sugars and d-alanine attached. Because they are negatively charged, teichoic acids are partially responsible for the negative charge of the cell surface as a whole. There are two types of teichoic acids: **wall teichoic acid (WTA)**, covalently linked to peptidoglycan, and **membrane teichoic acid**, covalently linked to membrane glycolipid. Because the latter are intimately associated with lipids, they have been called **lipoteichoic acids (LTA**



A: Teichoic acid structure. The segment of a teichoic acid made of phosphate, glycerol, and a side chain, R. R may represent
d-alanine, glucose, or other molecules. **B:** Teichoic and lipoteichoic acids of the gram-positive envelope.

The **teichuronic acids** are similar polymers, but the repeat units include sugar acids (eg, *N*-acetylmannosuronic or d-glucosuronic acid) instead of phosphoric acids. They are synthesized in place of teichoic acids when phosphate is limiting.

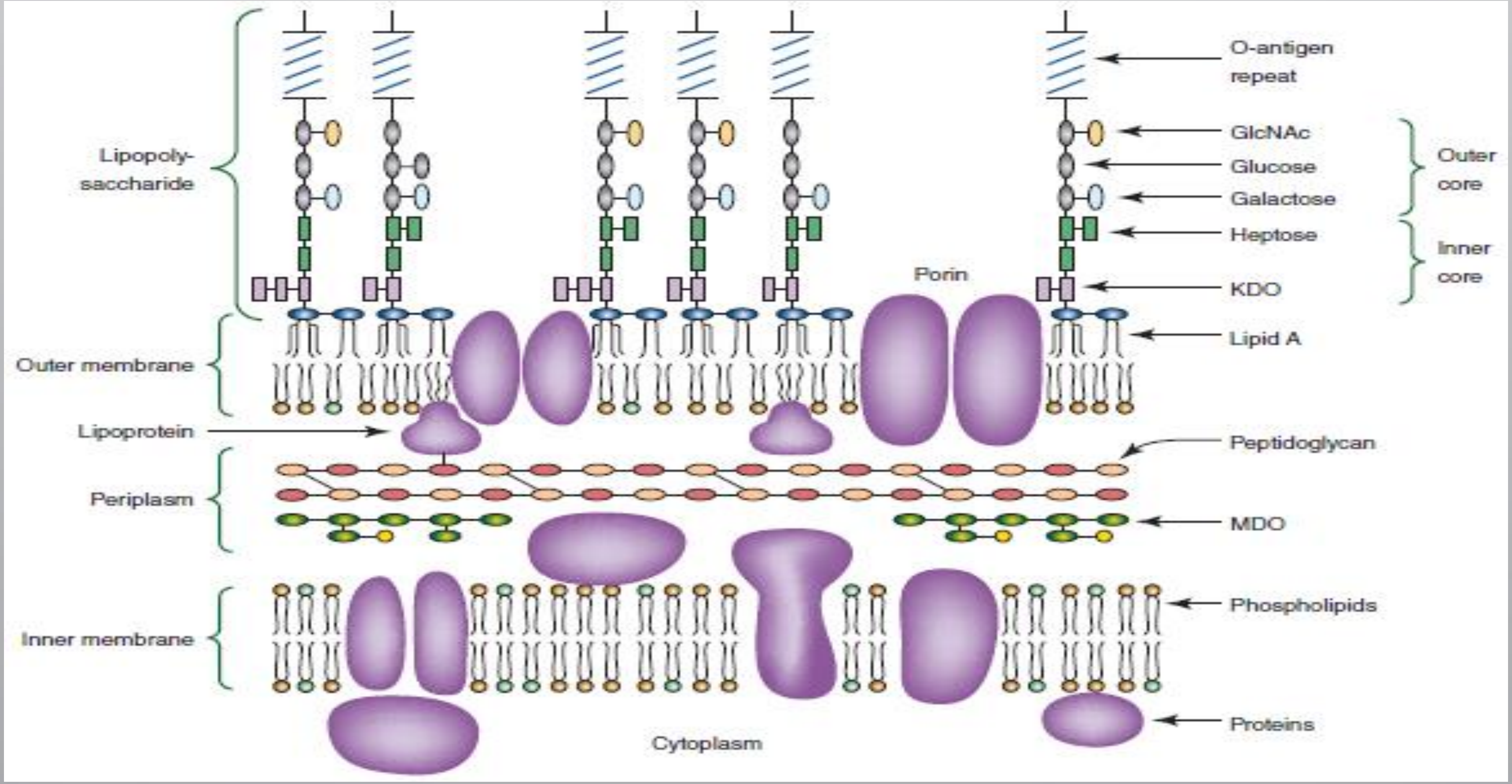
WTA and LTA make up a matrix that provides functions relating to the elasticity, porosity, and electrostatic properties of the envelope.

Special Components of Gram-Negative Cell Walls

Gram-negative cell walls contain three components that lie outside of the peptidoglycan layer: lipoprotein, outer membrane,and lipopolysacche

1. Outer membrane—The outer membrane is chemically distinct from all other biological membranes. It is a bilayered structure; its inner leaflet resembles in composition that of the cell membrane, and its outer leaflet contains a distinctive component, a **lipopolysaccharide (LPS)** . As a result, the leaflets of this membrane are asymmetrical, and the properties of this bilayer differ considerably from those of a symmetrical biologic membrane such as the cell membrane. the outer membrane has special channels, consisting of protein molecules called **porins** that permit the passive diffusion of low-molecular-weight hydrophilic compounds such as sugars, amino acids, and certain ions.

Large antibiotic molecules penetrate the outer membrane relatively slowly, which accounts for the relatively high antibiotic resistance of gram negative bacteria. The permeability of the outer membrane



Molecular representation of the envelope of a gram-negative bacterium. *Ovals* and *rectangles* represent sugar residues, and *circles* depict the polar head groups of the glycerophospholipids (phosphatidylethanolamine and phosphatidylglycerol).

2. Lipopolysaccharide (LPS)—The LPS of gram-negative cell walls consists of a complex glycolipid, called lipid A, to which is attached a polysaccharide made up of a core and a terminal series of repeat units. The lipid A component is embedded in the outer leaflet of the membrane anchoring the LPS. LPS is synthesized on the cytoplasmic membrane and transported to its final exterior position. The presence of LPS is required for the function of many outer membrane proteins. **Lipid A** consists of phosphorylated glucosamine disaccharide units to which are attached a number of long-chain fatty acids. and B is similar in all gram-negative species that have LPS and includes two characteristic sugars, **ketodeoxyoctanoic acid (KDO)** and a heptose.

Each species, however, contains a unique repeat unit, The repeat units are usually linear trisaccharides or branched tetra- or pentasaccharides. The repeat unit is referred to as the O antigen. The hydrophilic carbohydrate chains of the O-antigen cover the bacterial surface and exclude hydrophobic compounds.

- Lipopolysaccharide, which is extremely toxic to animals, has been called the **endotoxin** of gram-negative bacteria because it is firmly bound to the cell surface and is released only when the cells are lysed. When LPS is split into lipid A and polysaccharide, all of the toxicity is associated with the former.

The periplasmic space—The space between the inner and outer membranes, called the **periplasmic space**, contains the peptidoglycan layer and a gel-like solution of proteins. The periplasmic space is approximately 20–40% of the cell volume, which is far from insignificant. The periplasmic proteins include binding proteins for specific substrates (eg, amino acids, sugars, vitamins, and ions), hydrolytic enzymes. alkaline phosphatase and 52-nucleotidase) that break down nontransportable substrates into transportable ones, and detoxifying enzymes (eg, β-lactamase and aminoglycoside phosphorylase) that inactivate certain antibiotics.

Surface appendages

Capsule & Glycocalyx

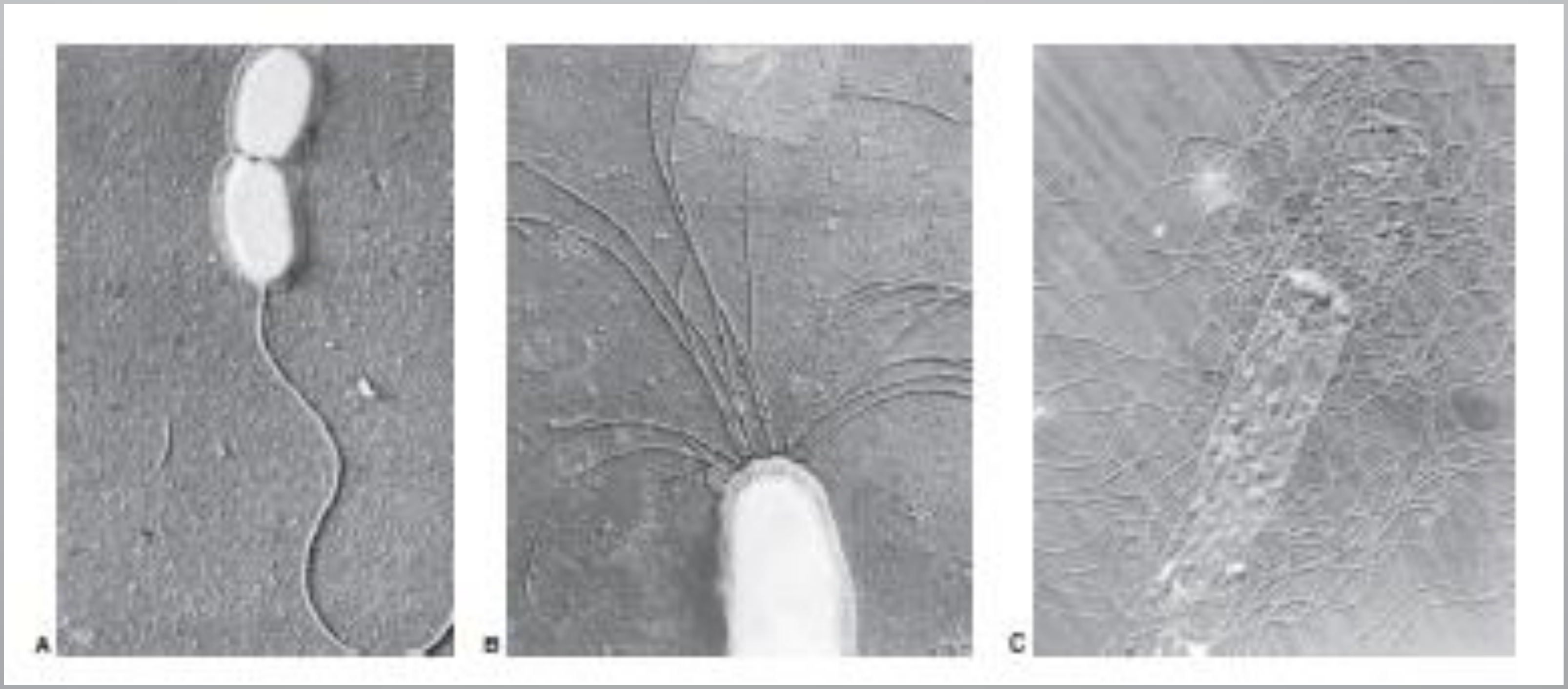
Many bacteria synthesize large amounts of extracellular polymer when growing in their natural environments. With one known exception (the poly-D-glutamic acid capsules of *Bacillus anthracis* and *Bacillus licheniformis*), the extracellular material is polysaccharide .The terms **capsule** and **slime layer** are frequently used to describe polysaccharide layers; the more inclusive term **glycocalyx** is also used. Glycocalyx is defined as the polysaccharide-containing material lying outside the cell.

The capsule contributes to the invasiveness of pathogenic bacteria—encapsulated cells are protected from phagocytosis unless they are coated with anticapsular antibody. The glycocalyx plays a role in the adherence of bacteria to surfaces in their environment, including the cells of plant and animal hosts.

Flagella

Bacterial flagella are thread-like appendages composed entirely of protein, 12–30 nm in diameter. They are the organs of locomotion for the forms that possess them. Three types of arrangement are known: **monotrichous** (single polar flagellum), **lophotrichous** (multiple polar flagella), and **peritrichous** (flagella distributed over the entire cell).

Bacterial flagellation



monotrichous **Polytrichous** **peritrichous**

A bacterial flagellum is made up of several thousand molecules of a protein subunit called **flagellin**. In a few organisms (eg, Caulobacter), flagella are composed of two types of flagellin, but in most, only a single type is found. The flagellum is formed by the aggregation of subunits to form a helical structure.

Pili (Fimbriae)

Many gram-negative bacteria possess rigid surface appendages called **pili** (L "hairs") or **fimbriae** (L "fringes"). They are shorter and finer than flagella; similar to flagella, they are composed of structural protein subunits termed **pilins**.

Some pili contain a single type of pilin, others more than one. Minor proteins termed **adhesins** are located at the tips of pili and are responsible for the attachment properties. Two classes can be distinguished: ordinary pili, which play a role in the adherence of symbiotic and pathogenic bacteria to host cells, and sex pili, which are responsible for the attachment of donor and recipient cells in bacterial conjugation. Pili are illustrated in Figure 2-27, in which the sex pili have been coated with phage particles for which they serve as specific receptors.

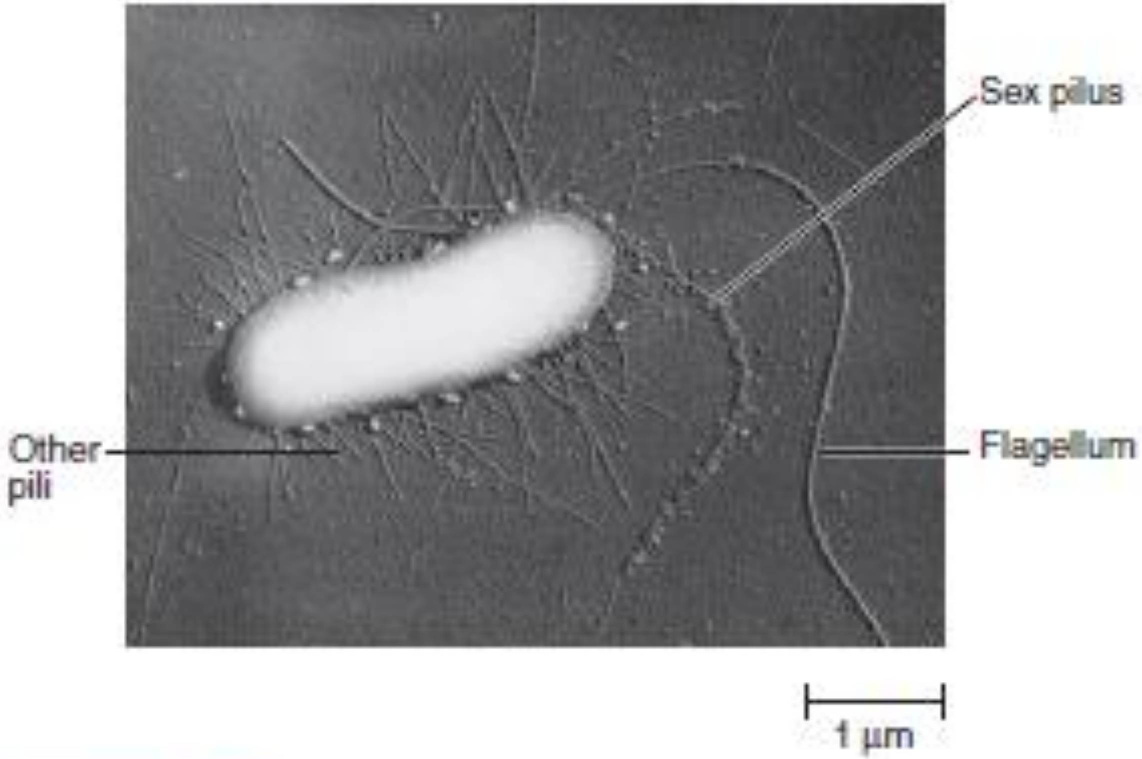


FIGURE 2-27 Pili. Pili on an *Escherichia coli cell*. The short pili (fimbriae) mediate adherence; the sex pilus is involved in DNA transfer. (Courtesy of Dr. Charles Brinton, Jr.)