Microbial physiology

The biosphere has been shaped both by physical events and by interactions with the organisms that occupy it. Among living organisms, prokaryotes are much more metabolically diverse than eukaryotes and can also thrive under a variety of extreme conditions where eukaryotes cannot. This is possible because of the wealth of genes, metabolic pathways and molecular processes that are unique to prokaryotic cells. For this reason, prokaryotes are very important in
the cycling of elements, including carbon, nitrogen, sulfur and phosphorus, as well as metals and metalloids such as copper, mercury, selenium, arsenic and chromium. A full understanding of the complex biological phenomena that occur in the biosphere therefore requires a deep knowledge of the unique biological processes that occur in this vast prokaryotic world.

It is widely accepted that less than 1% of prokaryotes have been cultivated in pure culture under laboratory conditions. The development of new sequencing techniques has allowed us to obtain genomic information from the multitudes of unculturable prokaryotic species and complex microbial populations that exist in nature. Such information might provide a basis for the development of new cultivation techniques. Elucidation of the function of unknown genes through a better understanding of biochemistry and physiology could ultimately result in a fuller understanding of the complex biological phenomena occurring in the biosphere.

The physiology of fungal cells impacts significantly on the environment, industrial processes, and human health. In relation to ecological aspects, the bio- geochemical cycling of carbon in nature would not be possible without the participation of fungi acting as primary decomposers of organic material. Furthermore, in agricultural operations fungi play important roles as mutualistic symbionts, pathogens, and saprophytes, where they mobilize nutrients and affect the physicochemical environment, or can be exploited as agents of biocontrol or as biofertilizers. Fungal metabolism is also responsible for the detoxification of organic pollutants and for bioremediating heavy metals and other recalcitrant chemicals in the environment (including wastewaters and ground waters). The production of many economically important industrial commodities relies on the exploitation of yeast and fungal

metabolism and these include such diverse products as whole foods, food additives, fermented beverages, antibiotics, probiotics, pigments, pharmaceuticals, biofuels, enzymes, vitamins, organic and fatty acids, and sterols. More negatively, fungi can cause considerable disease, spoil- age, and decay of important artifacts, commodities, and materials, buildings, and of course food supplies.

Like all organisms, microorganisms grow, metabolize and replicate utilizing materials available from the environment. Such materials include those chemical elements required for structural aspects of cellular composition and metabolic activities such as enzyme regulation and redox processes. To understand bacterial metabolism, it is therefore helpful to know the chemical composition of the cell and component structures.

Even a superficial examination of the microbial world shows that procaryotes are one of the most important groups by any criterion: numbers of organisms, general ecological importance, or practical impnumberortance for humans. Indeed, much of our understanding of phenomena in biochemistry and molecular biology comes from research on procaryotes. Although considerable space in this text is devoted to eucaryotic microorganisms, the major focus is on procaryotes. There are two quite different groups of procaryotes: *Bacteria* and *Archaea*. Although considerably less is known about archaeal cell structure and biochemistry, certain features distinguish the two domains. The word prokaryote will be used in a general sense to include both the *Bacteria* and *Archaea.*

Structure of microbial cells

Microorganisms are grouped into either prokaryotes or eukaryotes according to their cellular structure. With only a few exceptions, prokaryotic cells do not have subcellular organelles separated from the cytoplasm by phospholipid membranes such as the nuclear and mitochondrial membranes. Organelles like the nucleus, mitochondria and endoplasmic reticulum are only found in eukaryotic cells.

Archaea

These prokaryotes are quite different from eubacteria and have some features, especially aspects of the transcription and translation machinery associated with protein synthesis that are similar to eukaryotic cells. Most archaeans live in extreme environments similar to those that early life forms are thought to have endured.

The ***Archaea*** [Greek *archaios,* ancient] Like the *Bacteria,* the *Archaea* are quite diverse, both in morphology and physiology. They can stain either gram positive or gram negative and may be spherical, rod-shaped, spiral, lobed, cuboidal, triangular, plate-shaped, irregularly shaped, or pleomorphic. Some are single cells, whereas othersform filaments or aggregates. They range in diameter from 0.1 to over 15 *M*m, and some filaments can grow up to 200 *M*m in length.
Multiplication may be by binary fission, budding, fragmentation, or other mechanisms. The *Archaea* are just as diverse physiologically. They can be aerobic, facultatively anaerobic, or strictly anaerobic. Nutritionally they range from chemolithoautotrophs to organotrophs. They include psychrophiles, mesophiles, and hyperthermophiles that can grow above 100°C.
The types of environments where archaea have most often been found include areas with either very high or low temperatures or pH, concentrated salts, or completely anoxic. These are generally referred to as "extreme environments." However, terms such as extreme and hypersaline reflect a human perspective, meaning that they are situations where humans could not survive. On the contrary, most of the Earth (the oceans) is an "extreme environment" where it is very cold (about 4°C), dark, and under high pressure. Many archaea are well adapted to these environments, where they can grow to high numbers. For instance, archaea constitute at least 34% of the procaryotic biomass in at least some Antarctic coastal waters. In some hypersaline environments, their populations become so dense that the brine is red with archaeal pigments. Some archaea are symbionts in the digestive tracts of animals. Archaeal gene sequences have been found in soil and temperate and tropical ocean surface waters.

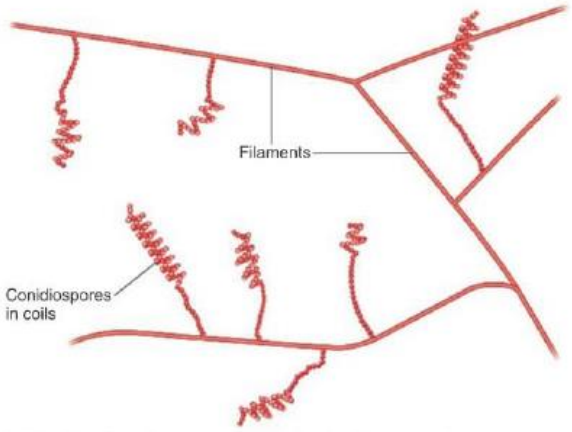
Actinomycetes

Filamentous microorganisms like filamentous fungi (from the Greek actina = ray; myces: filaments), are very common inhabitants in soil, where a filamentous pattern of growth has advantages. The filamentous organism can bridge water-free gaps between soil particles to move to a new nutritional site. This morphology also increases the organism ability to absorb nutrients in the highly competitive soil environment. The genera *Streptomyces*, *Frankia*, *Actinomyces,* and *Nocardia* are often informally called actinomycetes because they have a radiate, or starlike, form of growth by reason of their often-branching filaments.

Superficially, their morphology resembles that of filamentous fungi; however, the actinomycetes are prokaryotic cells, and their filaments have a diameter much smaller than that of the eukaryotic molds. Some actinomycetes further resemble molds by their possession of externally carried asexual spores that are used for reproduction.

The "earthy" smell of soil is caused by actinomycetes. Geosmin is an organic compound ($C_{12}H_{22}O$) with a distinct earthy flavor and aroma produced by Actinomycetes.

Certain *actinomycetes* reproduce by producing chains of conidiospores carried externally at the tips of the filaments. A few filamentous species simply fragment, and the fragments initiate the growth of new cells.



(a) Drawing of a typical streptomycete showing filamentous, branching growth with asexual reproductive conidiospores at the filament tips

Certain *actinomycetes* reproduce by producing chains of conidiospores carried externally at the tips of the filaments. A few filamentous species simply fragment, and the fragments initiate the growth of new cells.

Prokaryotic cell structure:

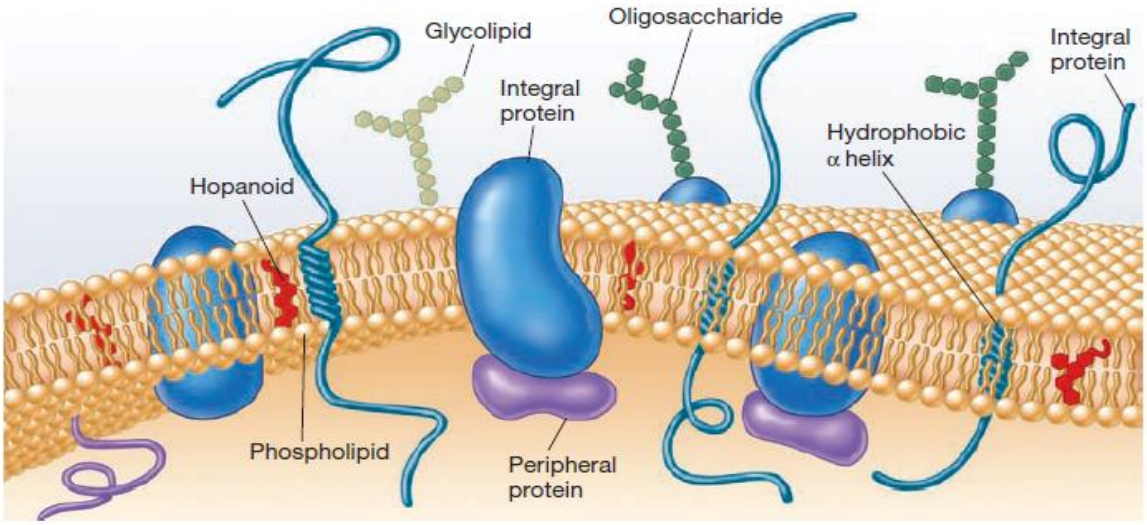
Bacteria vary in size as much as in shape. *Escherichia coli* is a rod of about average size, 1.1 to 1.5 µm wide by 2.0 to 6.0 µm long. Nanobacteria range from around 0.2 µm to less than 0.05 µm in diameter. Only a few strains have been cultured, and these appear to be very small, bacteria-like organisms. The discovery of nanobacteria was quite surprising because theoretical calculations predicted that the smallest cells were about 0.14 to 0.2 µm in diameter. At the other end of the continuum are bacteria such as the spirochaetes, which can reach 500 µm in length, and the photosynthetic bacterium *Oscillatoria,* which is about 7 µm in diameter (the same diameter as a red blood cell).

Generally, procaryotic cells are supposed to be smaller than eucaryotic cells. Procaryotes grow extremely rapidly compared to most eucaryotes, *Thiomargarita*

namibiensis is a spherical bacterium, between 100 and 750 µm in diameter, that often forms chains of cells enclosed in slime sheaths.
The discovery of these procaryotes greatly weakens the distinction between procaryotes and eucaryotes based on cell size. They are certainly larger than a normal eucaryotic cell. *Nanochlorum eukaryotum* is only about 1 to 2 µm in diameter

Plasma membrane

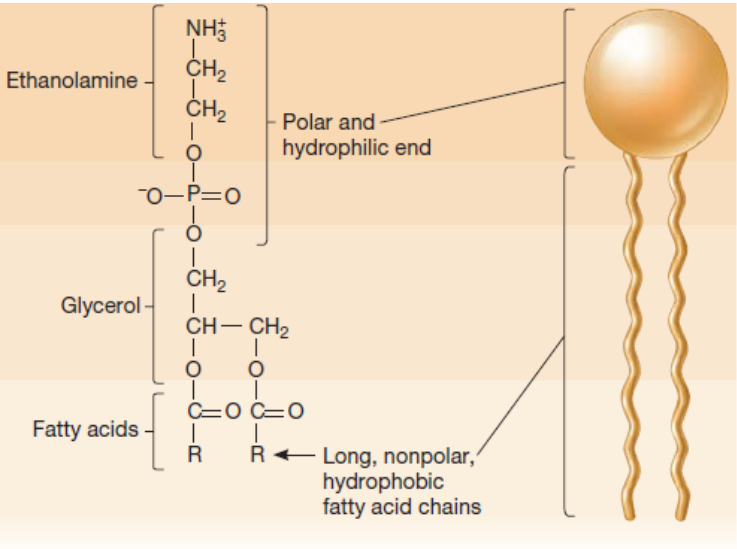
The most widely accepted model for membrane structure is the **fluid mosaic model** of Singer and Nicholson, which proposes that membranes are lipid bilayers within which proteins float. The model is based on studies of eukaryotic and bacterial membranes and a variety of experimental approaches were used to establish it. Transmission electron microscopy (TEM) studies were particularly important. When membranes are stained and examined by TEM, it can be seen that cell membranes are very thin structures, about 5 to 10 nm thick, and that they appear as two dark lines on either side of a non-stained interior. Within the lipid bilayer, small globular particles are visible; these have been suggested to be membrane proteins lying within the membrane lipid bilayer. Carbohydrates often are attached to the outer surface of plasma membrane proteins, where they have important functions.



Bacterial Membranes

Bacterial membranes are similar to eucaryotic membranes in that many of their amphipathic lipids are phospholipids, but they usually differ from eucaryotic membranes in lacking sterols (steroid-containing lipids) such as cholesterol.
However, many bacterial membranes contain sterol-like molecules called **hopanoids**. Hopanoids are synthesized from the same precursors as steroids, and like the sterols in eucaryotic membranes, they probably stabilize the membrane.

The emerging picture of bacterial plasma membranes is one of a highly organized and asymmetric system that also is flexible and dynamic. Numerous studies have demonstrated that lipids are not homogeneously distributed in the plasma membrane. Rather, there are domains in which particular lipids are concentrated. It has also been demonstrated that the lipid composition of bacterial membranes varies with environmental temperature in such a way that the membrane remains fluid during growth. For example, bacteria growing at lower temperatures will have fatty acids with lower melting points in their membrane phospholipids.
The chemical nature of membrane lipids is critical to their ability to form bilayers. The polar ends interact with water and are **hydrophilic;** the nonpolar **hydrophobic** ends are insoluble in water and tend to associate with one another. Two types of membrane proteins have been identified based on their ability to be separated from the membrane.

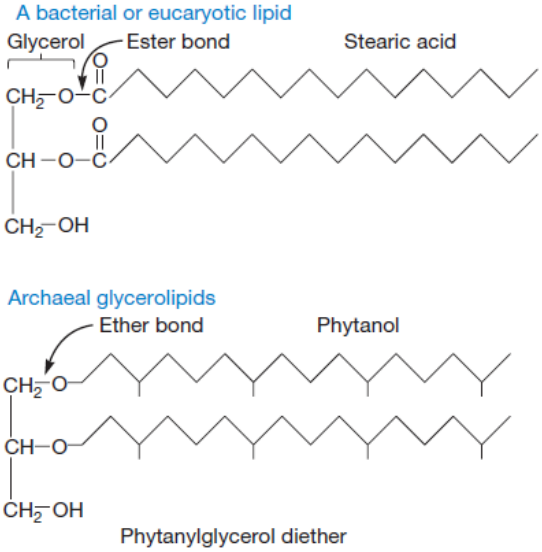


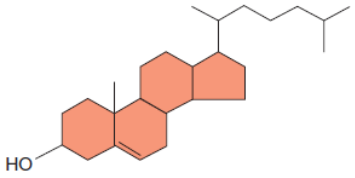
Archaeal Membranes

One of the most distinctive features of the *Archaea* is the nature of their membrane lipids. They differ from both *Bacteria* and *Eucarya* in having branched chain hydrocarbons attached to glycerol by ether links rather than fatty acids connected by ester links. Sometimes two glycerol groups are linked to form an extremely long tetraether. Usually the diether hydrocarbon chains are 20 carbons in length, and the tetraether chains are 40 carbons. Cells can adjust the overall length of the tetraethers by cyclizing the chains to form pentacyclic rings.
Sometimes two glycerol groups are linked to form an extremely long tetraether. Usually the diether hydrocarbon chains are 20 carbons in length, and the tetraether chains are 40 carbons. Cells can adjust the overall length of the tetra-ethers by cyclizing the chains to form pentacyclic rings.

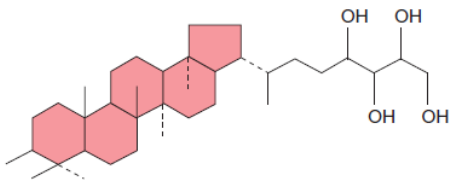
Phosphate-, sulfur- and sugar-containing groups can be attached to the third carbons of the di-ethers and tetraethers, making them polar lipids. These predominate in the membrane, and 70 to 93% of the membrane lipids are polar. The remaining lipids are nonpolar and are usually derivatives of squalene. Despite these significant differences in membrane lipids, the basic design of archaeal membranes is similar to that of *Bacteria* and eucaryotes there are two hydrophilic surfaces and a hydrophobic core. When C20 diethers are used, a regular bilayer membrane is formed. When the membrane is constructed of C40 tetraethers, a monolayer membrane with much more rigidity is formed. As might be expected from their need for stability, the membranes of extreme thermophiles such as *Thermoplasma* and *Sulfolobus*, which grow best at temperatures over 85°C, are almost completely tetraether monolayers.
Archaea that live in moderately hot environments have a mixed membrane containing some regions with monolayers and some with bilayers.

Plasma membrane infoldings are common in many bacteria and can become extensive and complex in photosynthetic bacteria such as the cyanobacteria and purple bacteria or in bacteria with very high respiratory activity, like the nitrifying bacteria. These internal membranous structures may be aggregates of spherical vesicles, flattened vesicles, or tubular membranes. Their function may be to provide a larger membrane surface for greater metabolic activity.

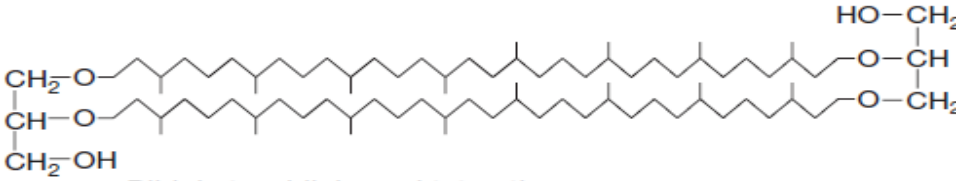




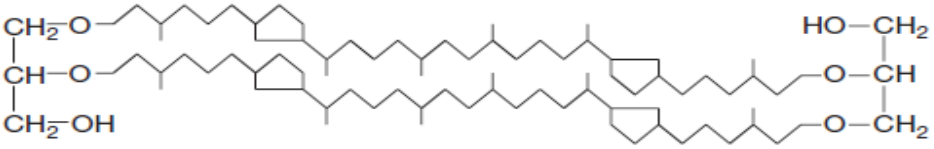
(a) Cholesterol (a steroid) is found in eucaryotes



(b) A bacteriohopanetetrol (a hopanoid), as found in bacteria



Dibiphytanyldiglycerol tetraether



Tetraether with bipentacyclic C_{40} biphytanyl chains

Figure 3.9 Archaeal Membrane Lipids. An illustration of the difference between archaeal lipids and those of *Bacteria*. Archaeal lipids are derivatives of isopranyl glycerol ethers rather than the glycerol fatty acid esters in *Bacteria*. Three examples of common archaeal glycerolipids are given.

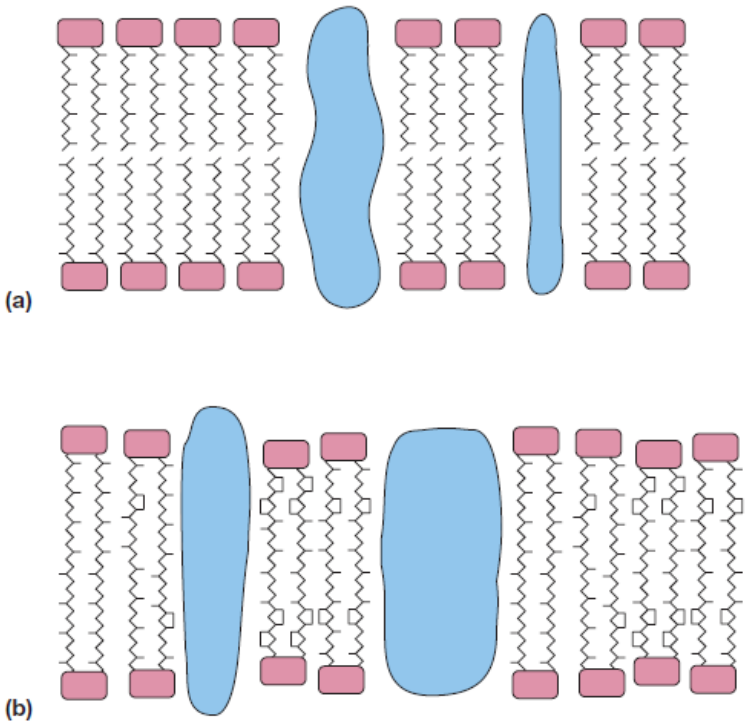


Figure 3.11 Examples of Archaeal Membranes. **(a)** A membrane composed of integral proteins and a bilayer of C_{20} diethers. **(b)** A rigid monolayer composed of integral proteins and C_{40} tetraethers.

The Cytoplasmic Matrix

The cytoplasmic matrix is the substance in which the nucleoid, ribosomes, and inclusion bodies are suspended. It lacks organelles bound by lipid bilayers (often called unit membranes), and is largely water (about 70% of bacterial mass is water). Until recently, it was thought to lack a cytoskeleton. The plasma membrane and everything within is called the **protoplast;** thus the cytoplasmic matrix is a major part of the protoplast.

Inclusion Bodies

Inclusion bodies, granules of organic or inorganic material that often are clearly visible in a light microscope, are present in the cytoplasmic matrix. These bodies usually are used for storage (e.g., carbon compounds, inorganic substances, and energy), and also reduce osmotic pressure by tying up molecules in particulate form. Some inclusion bodies lie free in the cytoplasm—for example, polyphosphate granules, cyanophycin granules, and some glycogen granules. Other inclusion bodies are enclosed by a shell about 2.0 to 4.0 nm thick, which is single-layered and may consist of proteins or a membranous structure composed of proteins and phospholipids.

The cell wall is the layer, usually fairly rigid, that lies just outside the plasma membrane. It is one of the most important prokaryotic structures for several reasons: it helps determine the shape of the cell; it helps protect the cell from osmotic lysis; it can protect the cell from toxic substances; and in pathogens, it can contribute to pathogenicity. The importance of the cell wall is reflected in the fact that relatively few procaryotes lack cell walls. Those that do have other features that fulfill cell wall function. The prokaryotic cell wall also is the site of action of several antibiotics. Therefore, it is important to understand its structure.
The cell walls of *Bacteria* and *Archaea* are distinctive and are another example of the important features distinguishing these organisms.

Microbial cell wall

Bacterial Cell Wall Structure

One important feature of the cell envelope is a space that is frequently seen between the plasma membrane and the outer membrane in electron micrographs of gram-negative bacteria, and is sometimes observed between the plasma membrane and the wall in gram-positive bacteria. This space is called the **periplasmic space.** The substance that occupies the periplasmic space is the **periplasm.** The nature of the periplasmic space and periplasm differs in gram-positive and gram-negative

bacteria. These differences are pointed out in the more detailed discussions that follow.

Peptidoglycan Structure

Peptidoglycan, or murein, is an enormous meshlike polymer composed of many identical subunits. The polymer contains two sugar derivatives, *N*-acetylglucosamine and *N*-acetylmuramic acid (the lactyl ether of *N*-acetylglucosamine), and several different amino acids. Three of these amino acids are not found in proteins: D-glutamic acid, D-alanine, and *meso*diaminopimelic acid. The presence of D-amino acids protects against degradation by most peptidases, which recognize only the L-isomers of amino acid residues.

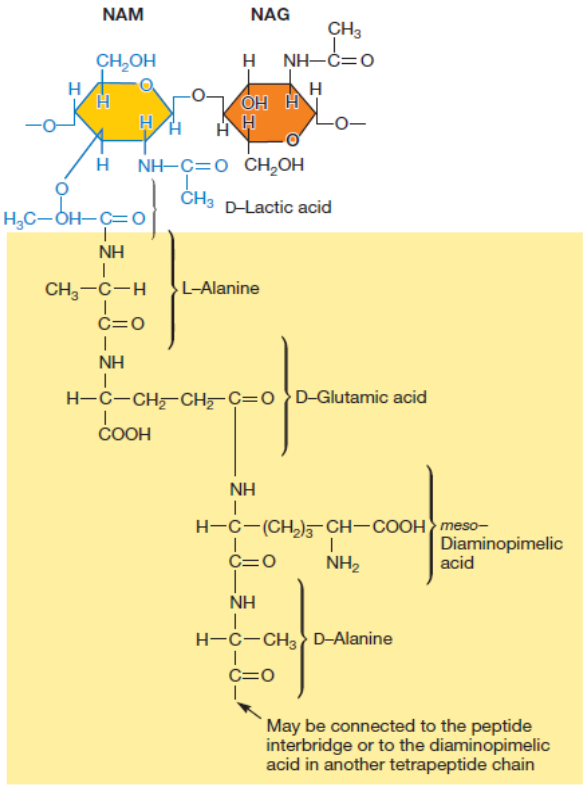


Figure 3.18 Peptidoglycan Subunit Composition. The peptidoglycan subunit of *E. coli,* most other gram-negative bacteria, and many gram-positive bacteria. NAG is *N*-acetylglucosamine. NAM is *N*-acetylmuramic acid (NAG with lactic acid attached by an ether linkage). The tetrapeptide side chain is composed of alternating D- and L-amino acids since *meso*-diaminopimelic acid is connected through its L-carbon. NAM and the tetrapeptide chain attached to it are shown in different shades of color for clarity.

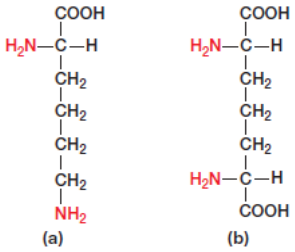


Figure 3.19 Diaminoacids Present in Peptidoglycan. **(a)** L-Lysine. **(b)** *meso*-Diaminopimelic acid.

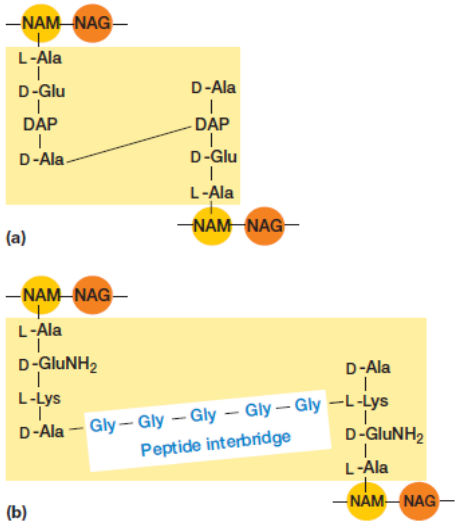


Figure 3.20 Peptidoglycan Cross-Links. **(a)** *E. coli* peptidoglycan with direct cross-linking, typical of many gram-negative bacteria. **(b)** *Staphylococcus aureus* peptidoglycan. *S. aureus* is a gram-positive bacterium. NAM is *N*-acetylmuramic acid. NAG is *N*-acetylglucosamine. Gly is glycine. Although the polysaccharide chains are drawn opposite each other for the sake of clarity, two chains lying side-by-side may be linked together (see figure 3.21).

The polymer is composed of alternating *N*-acetylglucosamine and *N*acetylmuramic acid residues. A peptide chain of four alternating D- and L-amino acids is connected to the carboxyl group of *N*acetylmuramic acid. Many bacteria replace *meso*-diaminopimelic acid with another diaminoacid, usually L-lysine

In order to make a strong, meshlike polymer, chains of linked peptidoglycan subunits must be joined by cross-links between the peptides. Often the carboxyl group of the terminal D-alanine is connected directly to the amino group of diaminopimelic acid, but a **peptide interbridge** may be used instead. Most gram-negative cell wall peptidoglycan lacks the peptide interbridge.

Gram-Positive Cell Walls

Gram-positive bacteria normally have cell walls that are thick and composed primarily of peptidoglycan. Peptidoglycan in grampositive bacteria often contains a peptide interbridge. In addition, gram-positive cell walls usually contain large amounts of **teichoic acids,** polymers of glycerol or ribitol joined by phosphate groups. Amino acids such as D-alanine or sugars like glucose are attached to the glycerol and ribitol groups. The teichoic acids are covalently connected to either the peptidoglycan itself or to plasma membrane lipids; in the latter case they are called lipoteichoic acids. Teichoic acids appear to extend to the surface of the peptidoglycan, and, because they are negatively charged, help give the gram-positive cell wall its negative charge.

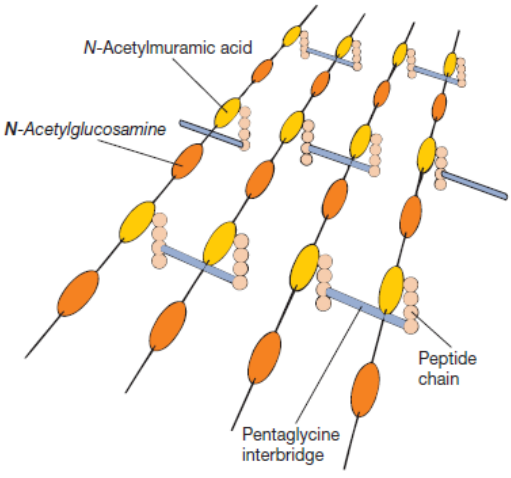


Figure 3.21 Peptidoglycan Structure. A schematic diagram of one model of peptidoglycan. Shown are the polysaccharide chains, tetrapeptide side chains, and peptide interbridges.

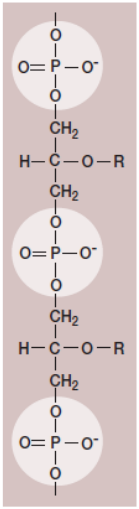


Figure 3.24 Teichoic Acid Structure. The segment of a teichoic acid made of phosphate, glycerol, and a side chain, R. R may represent D-alanine, glucose, or other molecules.

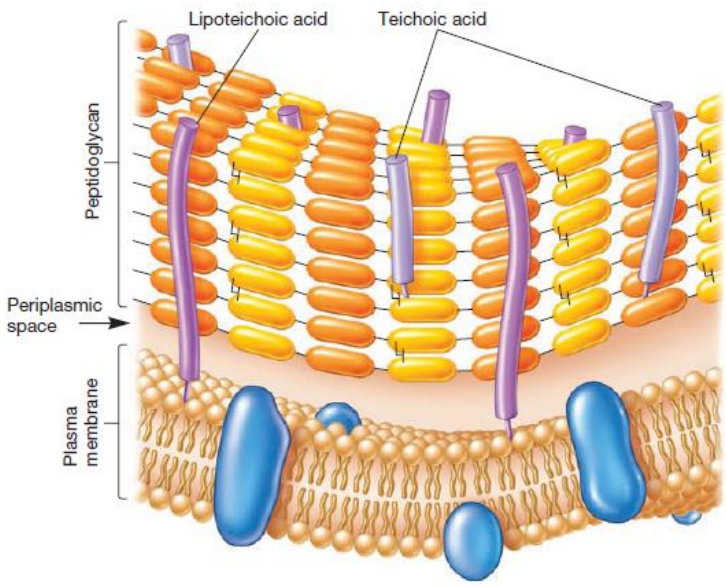


Figure 3.23 The Gram-Positive Envelope.

The functions of these molecules are still unclear, but they may be important in maintaining the structure of the wall. Teichoic acids are not present in gram-negative bacteria. The periplasmic space of gram-positive bacteria, when observed, lies between the plasma membrane and the cell wall and is smaller than that of gram-negative bacteria.

The periplasm has relatively few proteins; this is probably because the peptidoglycan sac is porous and any proteins secreted by the cell usually pass through it. Enzymes secreted by grampositive bacteria are called **exoenzymes.** They often serve to degrade polymeric nutrients that would otherwise be too large for transport across the plasma membrane. Those proteins that remain in the periplasmic space are usually attached to the plasma membrane. Staphylococci and most other gram-positive bacteria have a layer of proteins on the surface of their cell wall peptidoglycan.

These proteins are involved in the interactions of the cell with its environment. Some are noncovalently attached by binding to the peptidoglycan, teichoic acids, or other receptors. For example, the S-layer proteins bind noncovalently to polymers scattered throughout the wall. Many covalently attached proteins, such as the M protein of pathogenic streptococci, have roles in virulence, such as aiding in adhesion to host tissues and interfering with host defenses.

Gram-Negative Cell Walls

Gram-negative cell walls are much more complex than gram-positive walls. The thin peptidoglycan layer next to the plasma membrane and bounded on either side by the periplasmic space may constitute not more than 5 to 10% of the wall weight. In *E.*

coli it is about 2 nm thick and contains only one or two sheets of peptidoglycan. Some periplasmic proteins participate in nutrient acquisition—for example, hydrolytic enzymes and transport proteins. Some periplasmic proteins are involved in energy conservation. For example, the denitrifying bacteria, which convert nitrate to nitrogen gas, and bacteria that use inorganic molecules as energy sources (chemolithotrophs) have electron transport proteins in their periplasm. Other periplasmic proteins are involved in peptidoglycan synthesis and the modification of toxic compounds that could harm the cell.

The outer membrane lies outside the thin peptidoglycan layer and is linked to the cell in two ways. The first is by Braun's lipoprotein, the most abundant protein in the outer membrane. This small lipoprotein is covalently joined to the underlying peptidoglycan, and is embedded in the outer membrane by its hydrophobic end.

Possibly the most unusual constituents of the outer membrane are its **lipopolysaccharides (LPSs).** These large, complex molecules contain both lipid and carbohydrate, and consist of three parts:

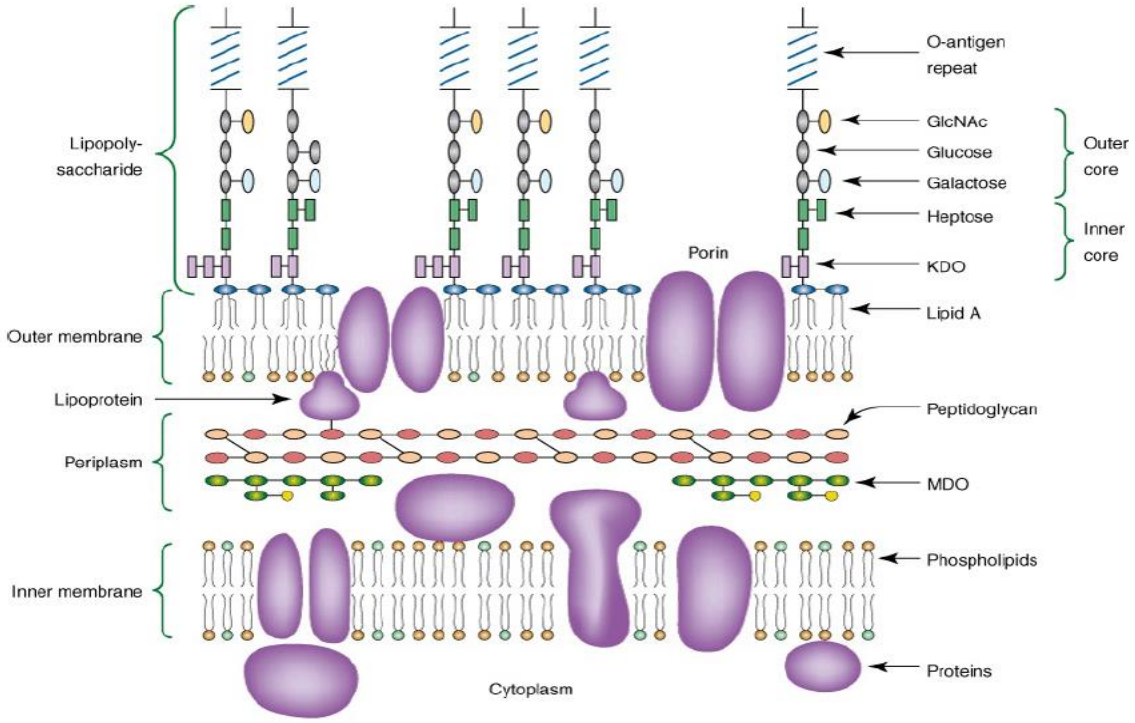
(1) lipid A
(2) the core polysaccharide
(3) the O side chain.

The **lipid A** region contains two glucosamine sugar derivatives, each with three fatty acids and phosphate or pyrophosphate attached. The fatty acids attach the lipid A to the outer membrane, while the remainder of the LPS molecule projects from the surface. The **core polysaccharide** is joined to lipid A.

The **O side chain** or **O antigen** is a polysaccharide chain extending outward from the core. It has several peculiar sugars and varies in composition between bacterial strains.

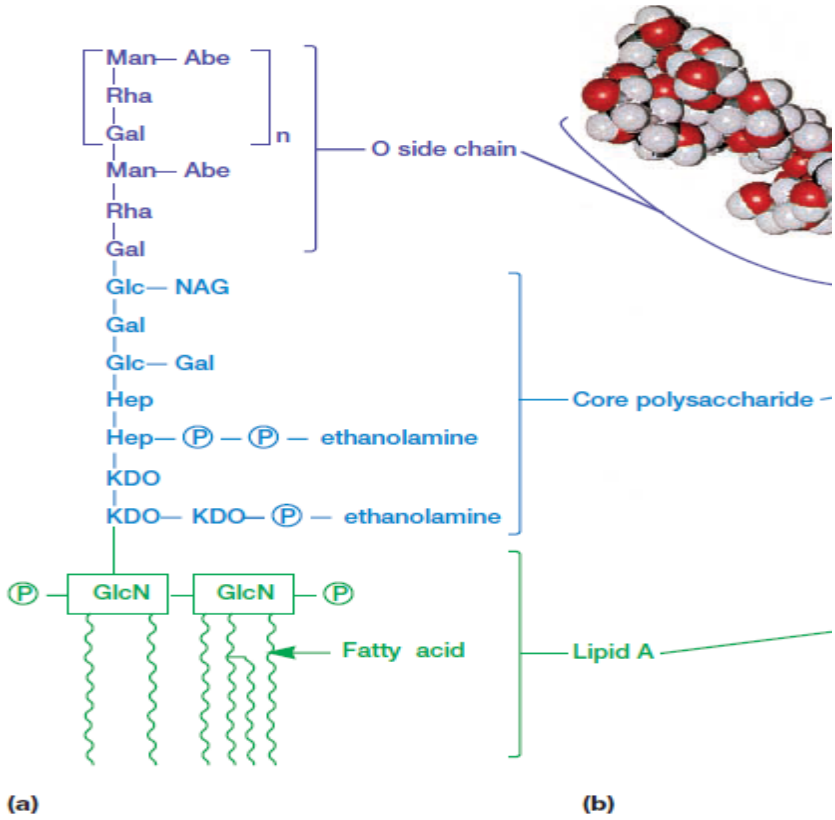
LPS has many important functions. Because the core polysaccharide usually contains charged sugars and phosphate, LPS contributes to the negative charge on the bacterial surface. As a major constituent of the exterior leaflet of the outer membrane, lipid A also helps stabilize outer membrane structure. LPS may contribute to bacterial attachment to surfaces and biofilm formation. A major function of LPS is that it aids in creating a permeability barrier. The geometry of LPS and interactions between neighboring LPS molecules are thought to restrict the entry of bile salts, antibiotics, and other toxic substances that might kill or injure the bacterium. LPS also plays a role in protecting pathogenic gram-negative bacteria from host defenses. The O side chain of LPS is also called the O antigen because it elicits an immune response. This response involves the production of antibodies that bind the strain-specific form of LPS that elicited the response. However, many gram negative bacteria are able to rapidly change the antigenic nature of their O side chains, thus thwarting host defenses. Importantly, the lipid A portion of LPS often

is toxic; as a result, the LPS can act as an endotoxin and cause some of the symptoms that arise in gram-negative bacterial infections.



Despite the role of LPS in creating a permeability barrier, the outer membrane is more permeable than the plasma membrane and permits the passage of small molecules like glucose and other monosaccharides. This is due to the presence of **porin proteins**. Most porin proteins cluster together to form a trimer in the outer membrane.

Each porin protein spans the outer membrane and is more or less tube-shaped; its narrow channel allows passage of molecules smaller than about 600 to 700 daltons. However, larger molecules such as vitamin B12 also cross the outer membrane. Such large molecules do not pass through porins; instead, specific carriers transport them across the outer membrane.



Archaeal Cell walls

Before they were distinguished as a unique domain of life, the *Archaea* were characterized as being either gram positive or gram negative. However, their staining reaction does not correlate as reliably with a particular cell wall structure as does the Gram reaction of *Bacteria*. Archaeal wall structure and chemistry differ from those of the *Bacteria*. Archaeal cell walls lack peptidoglycan and also exhibit considerable variety in terms of their chemical make-up. Some of the major features of archaeal cell walls are described in this section. Many archaea have a wall with a single, thick homogeneous layer resembling that in gram-positive bacteria.

These archaea often stain gram positive. Their wall chemistry varies from species to species but usually consists of complex heteropolysaccharides. For example, *Methanobacterium* and some other methane-generating archaea (methanogens) have walls containing a peptidoglycan-like polymer that has L-amino acids instead of D-amino acids in its cross-links, *N*-acetyltalosaminuronic acid instead of *N*-acetylmuramic acid, and β (1→3) glycosidic bonds instead of β (1→4) glycosidic bonds.

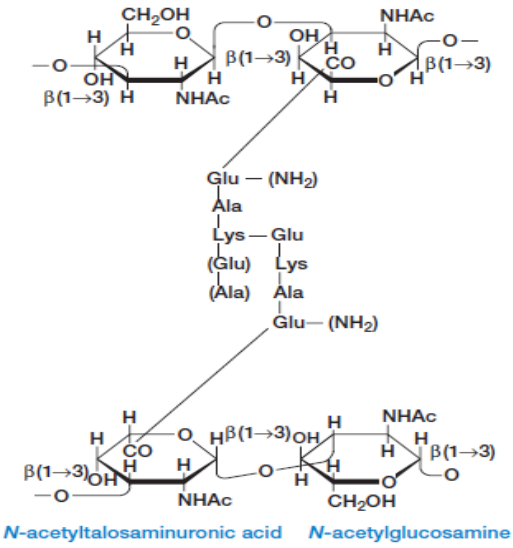


Figure 3.31 The Structure of Pseudomurein. The amino acids and amino groups in parentheses are not always present. Ac represents the acetyl group.

Table 4.2 Comparison of Procaryotic and Eucaryotic Cells

	Procaryotes		Eucaryotes
Property	***Bacteria***	***Archaea***	***Eukarya***
Organization of Genetic Material			
True membrane-bound nucleus	No	No	Yes
DNA complexed with histones	No	Some	Yes
Chromosomes	Usually one circular chromosome	Usually one circular chromosome	More than one; chromosomes are linear
Plasmids	Very common	Very common	Rare
Introns in genes	No	No	Yes
Nucleolus	No	No	Yes
Mitochondria	No	No	Yes
Chloroplasts	No	No	Yes
Plasma Membrane Lipids	Ester-linked phospholipids and hopanoids; some have sterols	Glycerol diethers and diglycerol tetraethers; some have sterols	Ester-linked phospholipids and sterols
Flagella	Submicroscopic in size; composed of one protein fiber	Submicroscopic in size; composed of one protein fiber	Microscopic in size; membrane bound; usually 20 microtubules in 9 + 2 pattern
Endoplasmic Reticulum	No	No	Yes
Golgi Apparatus	No	No	Yes
Peptidoglycan in Cell Walls	Yes	No	No
Ribosome Size	70S	70S	80S
Lysosomes	No	No	Yes
Cytoskeleton	Rudimentary	Rudimentary	Yes
Gas Vesicles	Yes	Yes	No

The fungi:

Fungi are widespread, non-photosynthetic microorganisms. The study of their metabolites and metabolism has made many contributions to the overall development of chemistry.
Based on their lifestyle, fungi may be circumscribed by the following set of characteristics:

1. **Nutrition**. Heterotrophic (lacking photosynthesis), feeding by absorption rather than ingestion.

2. **Vegetative state**. On or in the substratum, typically as a non-motile mycelium of hyphae showing internal protoplasmic streaming. Motile reproductive states may occur.

3. **Cell wall**. Typically present, usually based on glucans and chitin, rarely on glucans and cellulose (Oomycota).

4. **Nuclear status**. Eukaryotic, uni- or multinucleate, the thallus being homo- or heterokaryotic, haploid, dikaryotic or diploid, the latter usually of short duration (but exceptions are known from several taxonomic groups).

5. **Life cycle**. Simple or, more usually, complex.

6. **Reproduction**. The following reproductive events may occur: sexual (i.e. nuclear fusion and meiosis) and/or parasexual (i.e. involving nuclear fusion followed by gradual de-diploidization) and/or asexual (i.e. purely mitotic nuclear division).

7. **Propagules**. These are typically microscopically small spores produced in high numbers. Motile spores are confined to certain groups.

8. **Sporocarps**. Microscopic or macroscopic and showing characteristic shapes but only limited tissue differentiation.

9. **Habitat**. Ubiquitous in terrestrial and freshwater habitats, less so in the marine environment.

10. **Ecology**. Important ecological roles as saprotrophs, mutualistic symbionts, parasites, or hyperparasites.

11. **Distribution**. Cosmopolitan.

Although the biosynthetic pathways those fungi utilize to construct their metabolites have general features in common with those found in bacteria, plants and mammals, they differ in detail and the structures of the resultant natural products are often different.

Fungal cell wall composition

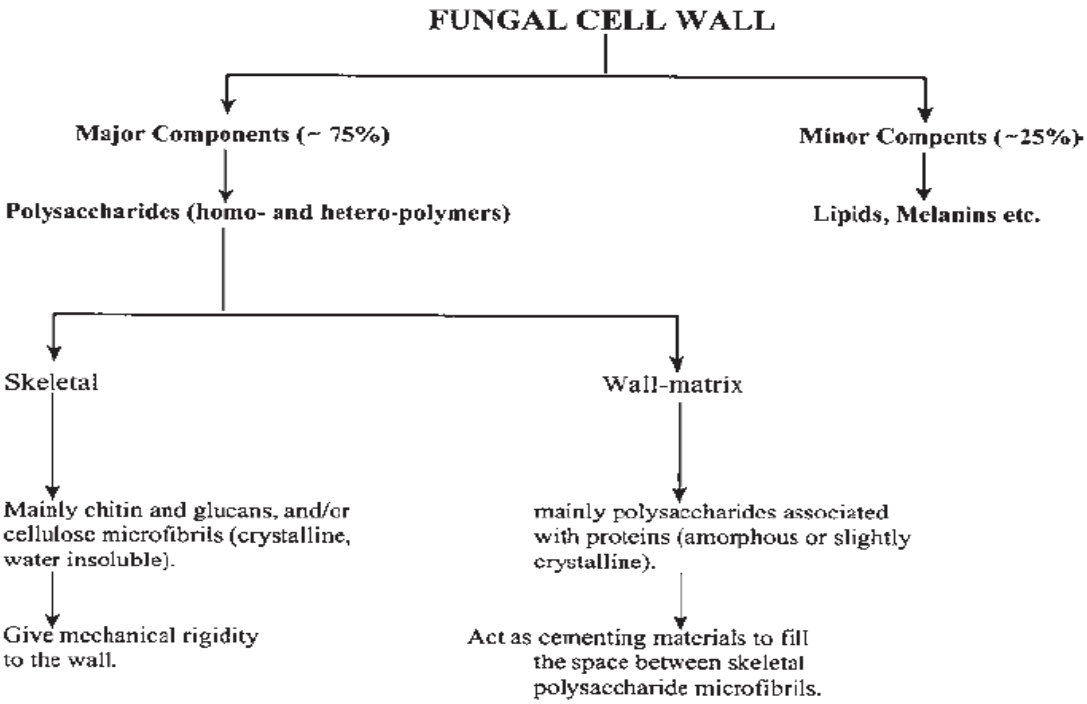
The fungal cell wall accounts for approximately 25% of the mycelial dry weight. Approximately 80% of the cell wall dry weight is comprised of polysaccharides. The remaining 20% is comprised of proteins, lipids, and various inorganic salts. The predominant carbohydrate polymers found in different fungi are various forms of glucans and chitin. These sugars, synthesized and positioned in a nonuniform, yet highly regulated manner provide the external skeleton of the hyphal cell and are synthesized mainly at the apical region of the growing hyphae. Nonetheless, additional components (in particular—cell wall-associated proteins) are involved in determining the cell surface properties of the growing hypha. Cell wall associated proteins are involved in the restriction of cell permeability to detrimental compounds and/or proteins present in the environment.

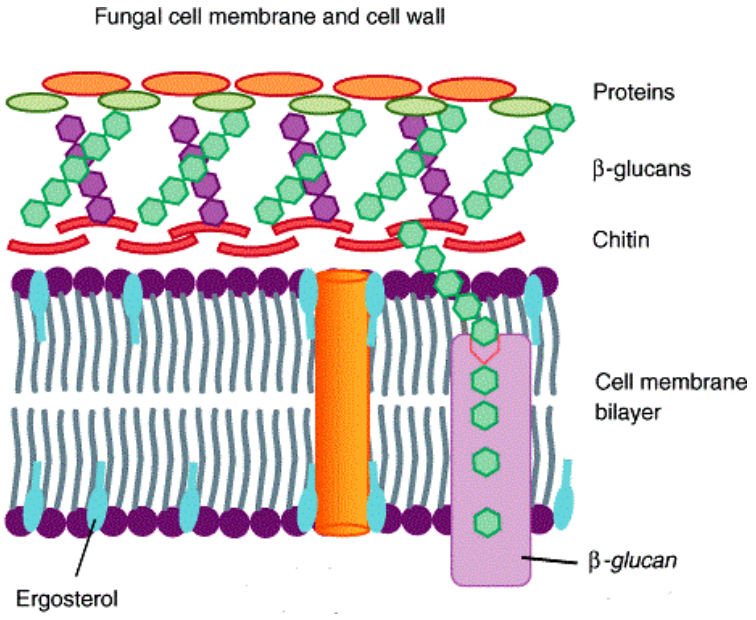
The fungal cell wall is a hardy structure that gives the cell its shape, protects it under the normally hypotonic environments, plays an important role in cell–cell interactions due to the presence of surface antigens, and acts as a site of extracellular enzymes with hydrolytic or metabolic activities.

In general, a fungal wall is composed of 70% or more polysaccharides and variable amounts of proteins, lipids, and melanins.

The fungal cell wall differs in its structural components both from the bacterial cell wall and mammalian cell. The plasma membrane is followed by three layers of cell wall material. From inside out these are:

- a chitin layer (polymer consisting mainly of unbranched chains of N-acetyl-D-glucosamine)
- a layer of β-1,3-glucan (zymosan)
- a layer of mannoproteins (mannose-containing glycoproteins) which are heavily glycosylated at the outside of the cell.





Fungal cell walls are mainly composed of polysaccharides. Two of them, β1- 3 glucan and chitin are common to all species in the fungal kingdom and constitute the skeleton of the cell wall. The three dimensional organization of the fungal cell wall has been however studied in very few fungal species. A comparison of the chemical composition of cell walls from different fungi demonstrates that a common skeletal core structure exists in almost all fungi. The major sterol in these is ergosterol rather than cholesterol which is found in mammalian systems. Inhibitors of the biosynthesis of these components can, therefore, be selectively fungicidal.

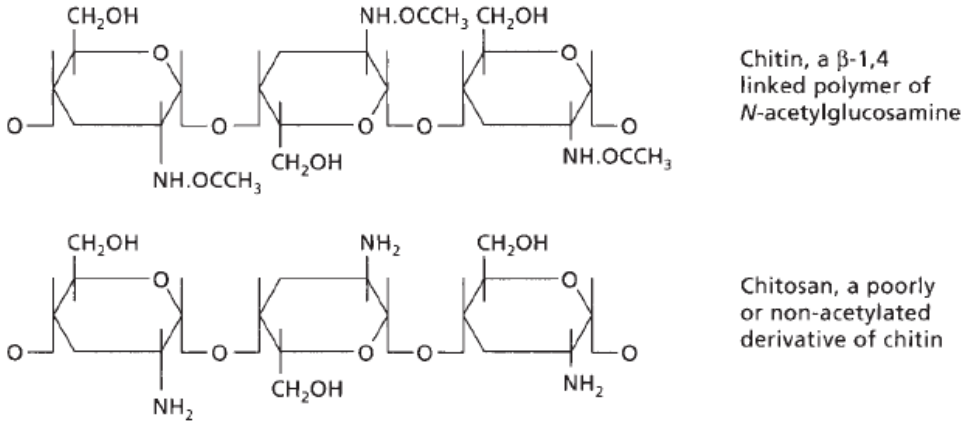
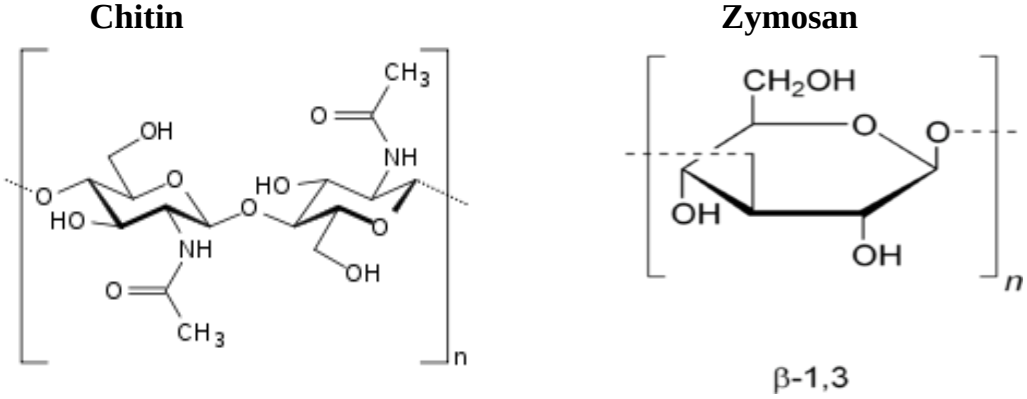
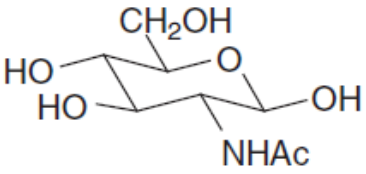
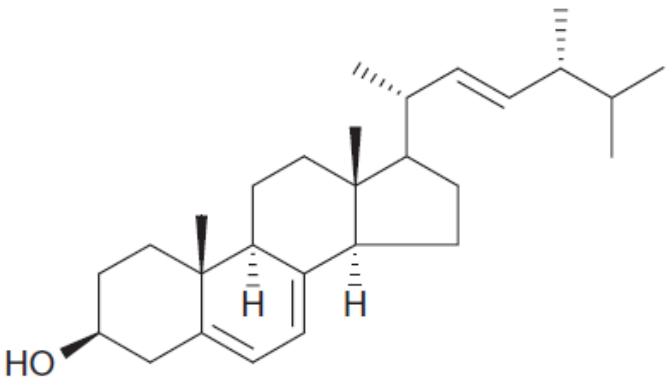


Fig. 7.11 Structure of chitin and its deacetylated derivative, chitosan.





a polymer of N-acetylglucosamine



ergosterol

This core skeleton is similar for both yeasts and moulds. It is composed of a branched β1-3 glucan to which chitin is linked through a β1-4 linkage to a non reducing end of the lateral β1-3 glucan chains. This fibrillar core is further decorated with amorphous polysaccharides that are alkali-soluble. In contrast to the structural polysaccharides, the composition of these polysaccharides varies with the species studied and has some taxonomical foundations. Among the most important amorphous polysaccharides, we can cite β1,6 glucans, α 1,3 glucans and mannans. Proteins of the cell wall do not play a role of linker in the structural organisation of the cell wall. Most cell wall proteins are in transit towards the external milieu. Some of the proteins that were originally anchored to the plasma membrane by a glycosylphosphatidylinositol (GPI) anchor play a role in remodeling cell wall polysaccharides whereas other GPI-proteins can become covalently bound to the cell wall polysaccharides; this latter class of proteins remaining at the surface of the cell wall to fullfil their biological function (in cell to cell interaction for example). This conclusion was confirmed by a chemogenomic comparative analysis between yeasts and moulds.

Table 1.2 Major polymers found in different taxonomic groups of fungi and fungus-like organisms, together with presence of perforate septa in these groups.

Taxonomic grouping	Fibrillar polymers	Matrix polymers	Perforate septa present or absent
Oomycetes (no longer considered to be true fungi)	β(1,3), β(1,6)-Glucan; cellulose	Glucan	Absent
Chytridomycetes	Chitin; glucan	Glucan	Absent
Zygomycetes	Chitin; chitosan	Polyglucuronic acid; glucuronomannoproteins	Absent
Basidiomycetes	Chitin; β(1,3)-β(1,6) glucans	α(1,3)-Glucan; xylomannoproteins	Present (mostly Dolipore)
Ascomycetes/ Deuteromycetes	Chitin; β(1,3)-β(1,6) glucans	α(1,3)-Glucan; galactomannoproteins	Present (mostly simple with large central pore)

Adapted from Deacon (2000); Carlile *et al.* (2001).

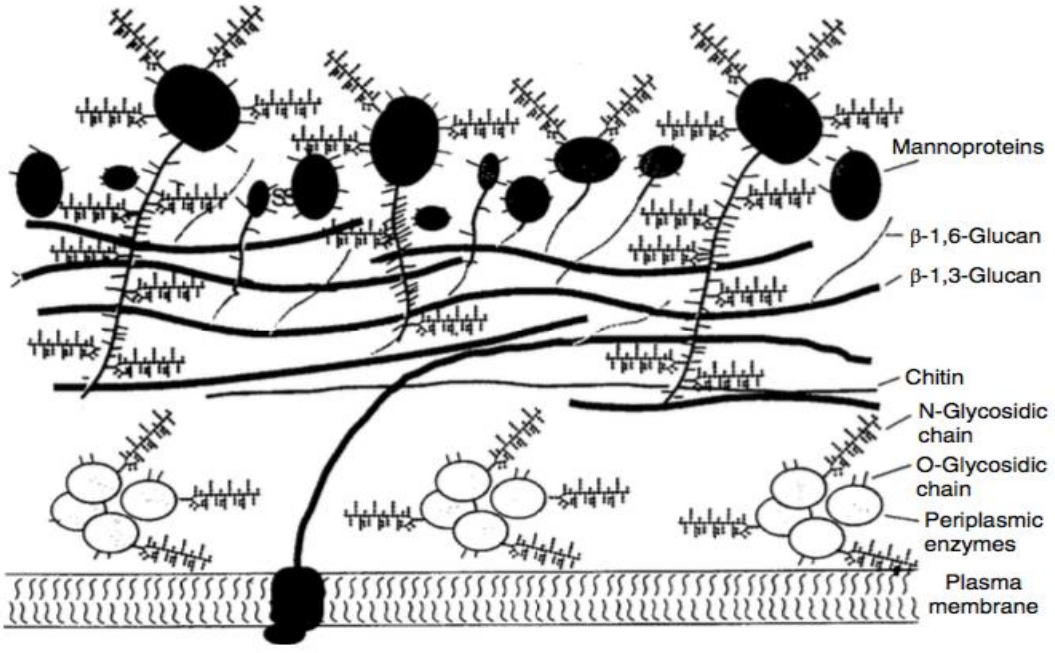


Figure 1.3 Cell envelope structure of the yeast *S. cerevisiae*. (From Walker (1998).)