Biochemistry Part II

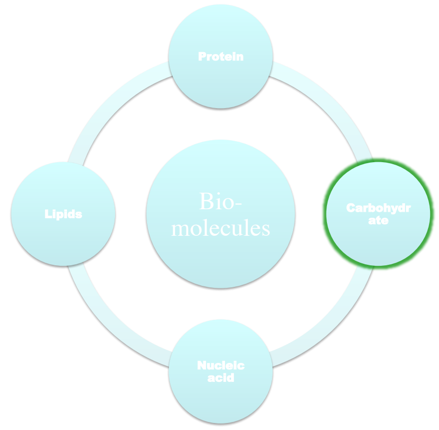
- Carbohydrate
- Glycobiology

- Nucleotides
- Nucleic acids

- Lipids

- Biological membranes and transport

- Biosignaling



Go back a little bit

- Elements in biochemistry
  - C
  - H
  - O
  - N
  - P
  - S

Features of functional group

- Hydroxyl (-OH)
- Methyl (C-, and H-)
- Nitrogen-containing (neuro-active, peptide bond)
- Thiol
- Phosphoryl
- Aldehyde, ketone

What is the most important concept in biochemistry?

How to read biochemistry

- Active reading vs. Passive reading
- Active reading
  - Convert text to questions
  - Ask questions during study
    - What (important facts, comparison, key concept that penetrate different chapters)
    - How (mechanism, structure-function relationship, experiments behind knowledge, discuss the many faces of one phenomenon)
    - Why (ideas that extract from biochemistry, logic, reasoning, significance)

Fact
Sphingomyelin is the principal lipid in neuron membrane

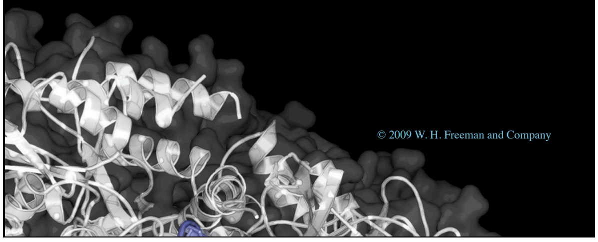
- "What" type question
  - Learn prefix/suffix/root words/etymology
  - To understand, not just memorize
- "why" type question
  - Functional requirement of neuron membrane
  - Reasoning from the viewpoint of evolution, logic of chemistry
  - May derive or deduce new knowledge

L E H N I N G E R
PRINCIPLES OF BIOCHEMISTRY

David L. Nelson
Michael M. Cox

FIFTH EDITION

7 | Carbohydrates and Glycobiology



CHAPTER 7
Carbohydrates and Glycobiology

Key topics about carbohydrates:

- Structures and names of monosaccharides
- Open-chain and ring forms of monosaccharides
- Structures and properties of disaccharides
- Biological function of polysaccharides
- Biological function of glycoconjugates

Exciting things about carbohydrate

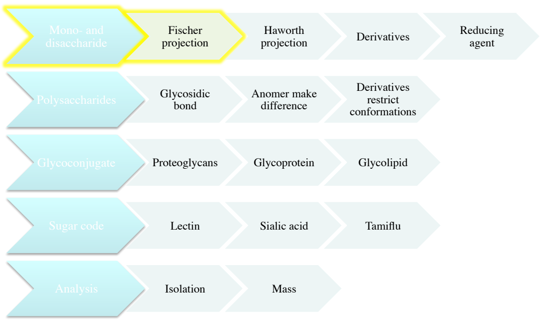
- The most abundant biomolecules
  - Starch as food (alpha-1,4 linked sugar)
  - Cellulose as structural materials (beta-1,4)
  - Both are explored for future fuel
- Both "how they linked" and "what are linked" are important
- Modify properties of other biomolecules
  - Glycoproteins
  - Antibiotics

Is sugar good or bad for health

- Sugar refers to "sucrose" most of time
- History for human to consume sugar is not long!
  - Suggested book
  改變世界的植物 董曉黎譯
  馬斯格雷夫 (Musgrave, Toby)
  Musgrave, Toby 高談文化, 2006

Why sugar is sweet

- From the viewpoint of biochemistry
  - It's the receptor!
  - Based on molecular recognition
  - What are the structural features of D-glucose, or sucrose
    - Hydrophilic side and hydrophobic side



Carbohydrates

- Named so because many have formula $C_n(H_2O)_n$
- Produced from CO_2 and H_2O via photosynthesis in plants
- Range from as small as glyceraldehyde (M_w = 90 g/mol) to as large as amylopectin (M_w = 200,000,000 g/mol)
- Fulfill a variety of functions including:
  - energy source and energy storage
  - structural component of cell walls and exoskeletons
  - informational molecules in cell-cell signaling
- Often covalently linked with proteins to form glycoproteins and proteoglycans

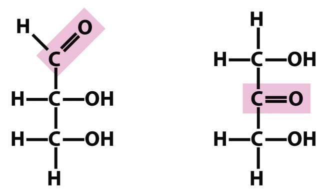
Definition of carbohydrate

- Polyhydroxy aldehyde, or ketone
- Monosaccharide contains a single polyhydroxy aldehyde, or ketone unit
- Disaccharides
  - Sucrose, maltose
- Oligosaccharides
- Polysaccharides
  - Starch, cellulose

Aldoses and Ketoses

An aldose contains an aldehyde functionality
A ketose contains a ketone functionality

Simplest monosaccharide 3 carbons, 0 or 1 chiral center



Glyceraldehyde, an aldotriose **Dihydroxyacetone, a ketotriose**

Figure 7-1a
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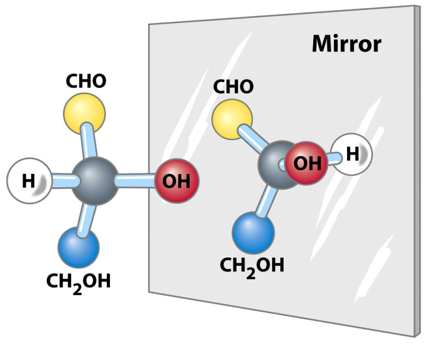
Enantiomers

- Enantiomers: stereoisomers that are non-superimposable mirror images
- In sugars that contain many chiral centers, only the one that is most distant from the carbonyl carbon is designated as D or L
- D and L isomers of a sugar are enantiomers
  - *e.g.* L and D glucose have the same water solubility
- Most hexoses in living organisms are D stereoisomers
- Some simple sugars occur in the L-form, such as L-arabinose



Ball-and-stick models

Figure 7-2 part 1
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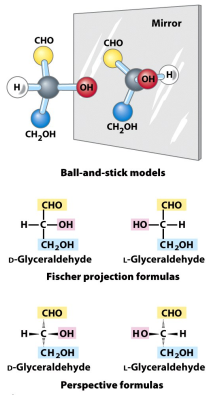

Figure 7-2
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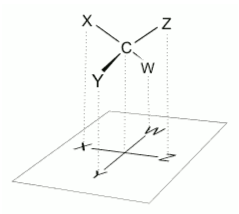
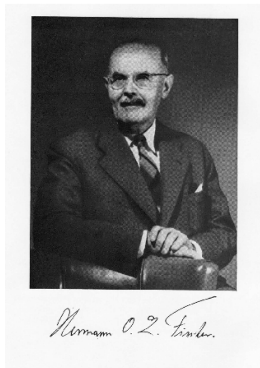
Fischer projection (Emil Fischer)



HERMANN OTTO LAURENZ FISCHER

Professor of Biochemistry
Berkeley



HERMANN OTTO LAURENZ FISCHER

December 16, 1888–March 9, 1960

BY W. M. STANLEY AND W. Z. HASSID

HERMANN OTTO LAURENZ FISCHER was born on December 16, 1888, in the university town of Würzburg in Bavaria and died on March 9, 1960, in the University of California Hospital in Los Angeles. He was the first of three sons of Emil and Agnes Fischer and was early exposed to academic surroundings since his father was Professor of Chemistry at the University of Würzburg. In 1892 the Fischer family moved to Berlin where Fischer's father, not yet forty years of age, succeeded to the chair of August Wilhelm von Hofmann and directed the activities of the Chemical Institute of Berlin University. Three years later Fischer's mother died and the three boys grew up in the rather lonely household of their widowed father who was greatly preoccupied with his teaching and research. However, Fischer remembered with pleasure the very informative conversations which the boys had with their father at lunchtime. During this period the Fischer boys went to the local *Gymnasium* where, Fischer recalls, "Latin, Greek, history and German were taught very well, mathematics somewhat and science very little." Fischer was given full freedom to select a profession but, of course, his early and continuing contacts with academic life and chemical research were quite influential. He retained early memories of a two-week visit within the Fischer household of Sir William Ram-

Diastereomers

- Diastereomers: stereoisomers that are not mirror images
- Diastereomers have different physical properties
  - *e.g.* water solubilities of threose and erythrose are different

Drawing Monosaccharides

- Chiral compounds can be drawn using perspective formulas
- However, chiral carbohydrates are usually represented by Fischer projections
- Horizontal bonds are pointing towards you; vertical bonds are projecting away from you

D-Glyceraldehyde L-Glyceraldehyde

Fischer projection formulas

Figure 7-2 part 2
Lehninger Principles of Biochemistry, Fifth Edition

D-Glyceraldehyde L-Glyceraldehyde

Perspective formulas

Figure 7-2 part 3
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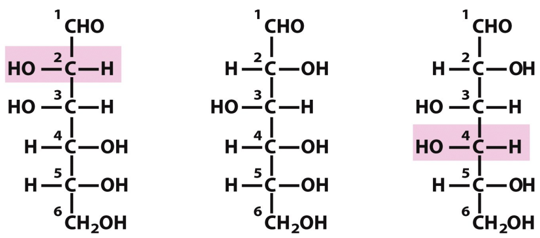
Epimers

- Epimers are two sugars that differ only in the configuration around one carbon atom



D-Mannose (epimer at C-2) D-Glucose D-Galactose (epimer at C-4)

Figure 7-4
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Structures to Know

- Ribose is the standard five-carbon sugar
- Glucose is the standard six-carbon sugar
- Galactose is an epimer of glucose
- Mannose is an epimer of glucose
- Fructose is the ketose form of glucose

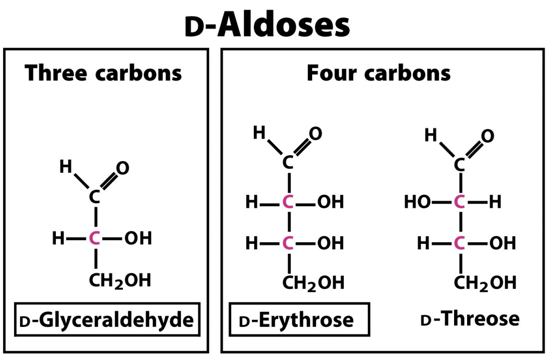

Figure 7-3a part 1
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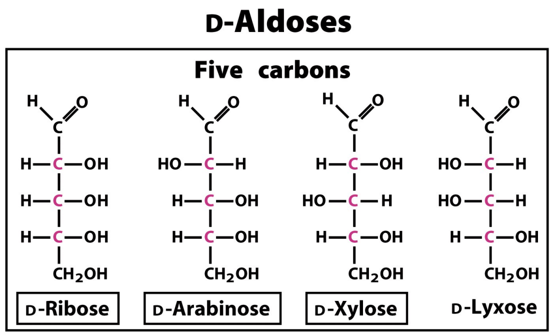

Figure 7-3a part 2
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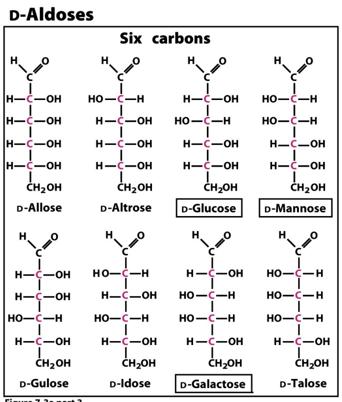

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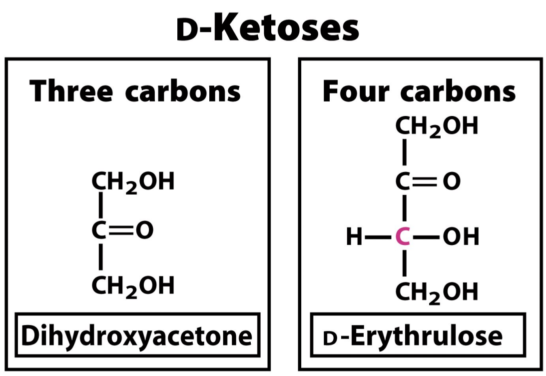

Figure 7-3b part 1
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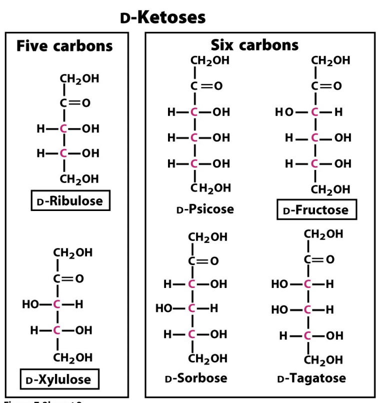

Figure 7-3b part 2
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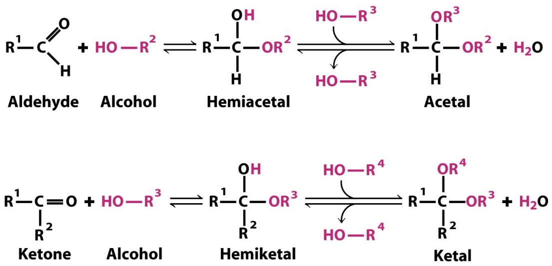
Hemiacetals and Hemiketals

- Aldehyde and ketone carbons are electrophilic
- Alcohol oxygen atom is a nucleophilic
- When aldehydes are attacked by alcohols, hemiacetals form
- When ketones are attacked by alcohols, hemiketals form



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Cyclization of Monosaccharides

- Pentoses and hexoses readily undergo intramolecular cyclization
- The former carbonyl carbon becomes a new chiral center, called the anomeric carbon
- The former carbonyl oxygen becomes a hydroxyl group; the position of this group determines if the anomer is α or β
- If the hydroxyl group is on the opposite side (trans) of the ring as the CH_2OH moiety the configuration is α
- In the hydroxyl group is on the same side (cis) of the ring as the CH_2OH moiety, the configuration is β

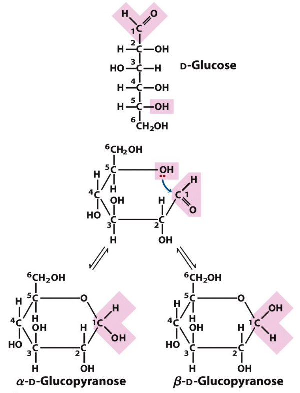

Figure 7-6
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Pyranoses and Furanoses

- Six-membered oxygen-containing rings are called pyranoses
- Five-membered oxygen-containing ring are called furanoses
- The anomeric carbon is usually drawn on the right side

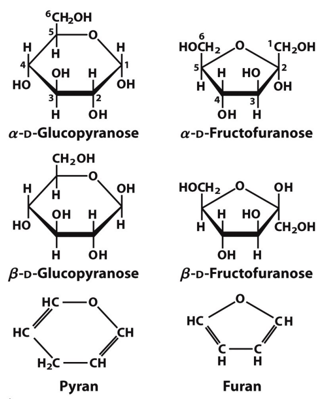

Figure 7-7
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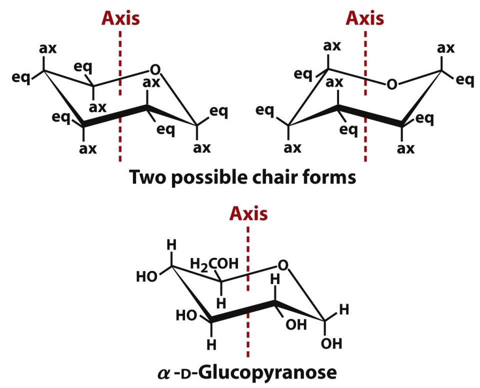

Figure 7-8
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Chain-ring Equilibrium and Reducing Sugars

- The ring forms exist in equilibrium with the open-chain forms
- Aldehyde can reduce Cu^{2+} to Cu^{+} (Fehling's test)
- Aldehyde can reduce Ag^{+} to Ag^{0} (Tollens' test)
- Allows to detect reducing sugars, such as glucose

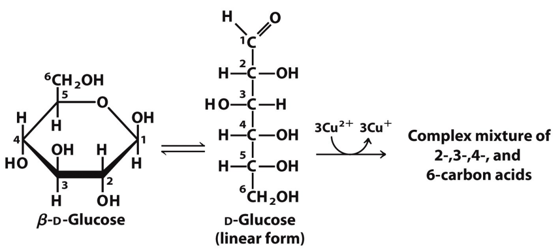

Figure 7-10
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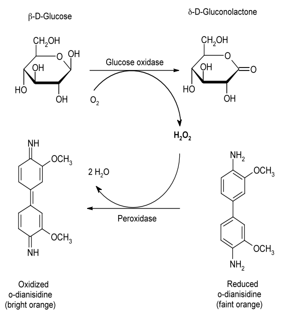
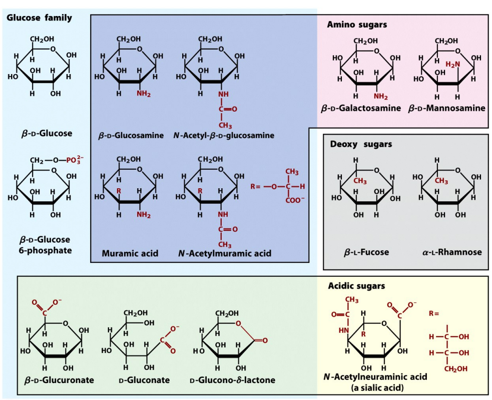
Colorimetric Glucose Analysis



- Nowadays, enzymatic methods are used to quantify reducing sugars such as glucose
  - The enzyme glucose oxidase catalyzes the conversion of glucose to glucono-δ-lactone and hydrogen peroxide
  - Hydrogen peroxide oxidizes organic molecules into highly colored compounds
  - Concentrations of such compounds is measured colorimetrically
- Electrochemical detection is used in portable glucose sensors

Important Hexose Derivatives

- New features acquired by modification
  - Hydroxyl group replaced by amine
    - Followed by adding acetyl group
  - Hydroxyl group is oxidized
  - Add new group (muramic)
  - Deoxy sugar



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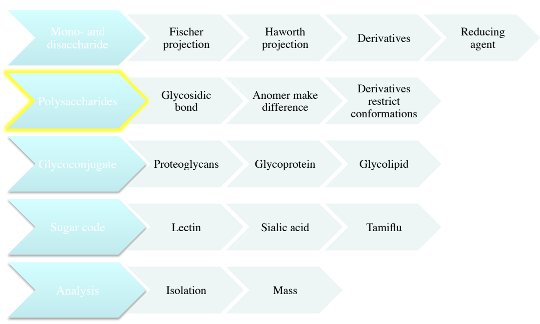

The Glycosidic Bond

- Two sugar molecules can be joined via a glycosidic bond between an anomeric carbon and a hydroxyl carbon
- The glycosidic bond (an acetal) between monomers is less reactive than the hemiacetal at the second monomer
- The disaccharide formed upon condensation of two glucose molecules via 1 → 4 bond is called maltose

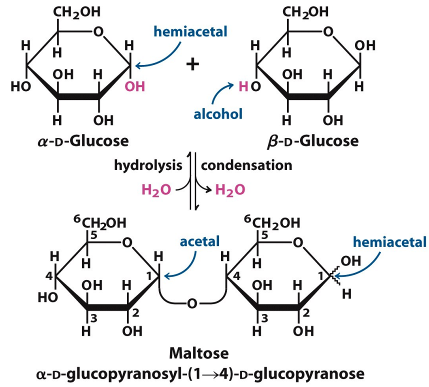

Figure 7-11
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Nonreducing disaccharides

- Two sugar molecules can be also joined via a glycosidic bond between two anomeric carbons
- The product has two acetal groups and no hemiacetals
- There is no reducing ends, this is a nonreducing disaccharide
- Trehalose is a constituent of hemolymph of insects
- Provides protection from drying
  - Resurrection plant (> 15 yrs)

Is there a "sequence" for polysaccharide?

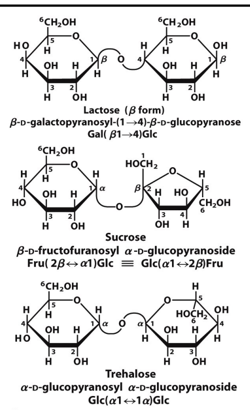

Figure 7-12
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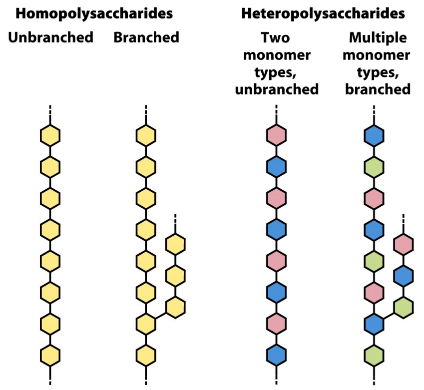
Polysaccharides

- Natural carbohydrates are usually found as polymers
- These polysaccharides can be
  - homopolysaccharides
  - heteropolysaccharides
- Polysaccharides do not have a defined molecular weight.
  - This is in contrast to proteins because unlike proteins, no template is used to make polysaccharides



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Glycogen

- Glycogen is a branched homopolysaccharide of glucose
  - Glucose monomers form ($\alpha 1 \rightarrow 4$) linked chains
  - Branch-points with ($\alpha 1 \rightarrow 6$) linkers every 8-12 residues
  - Molecular weight reaches several millions
  - Functions as the main storage polysaccharide in animals

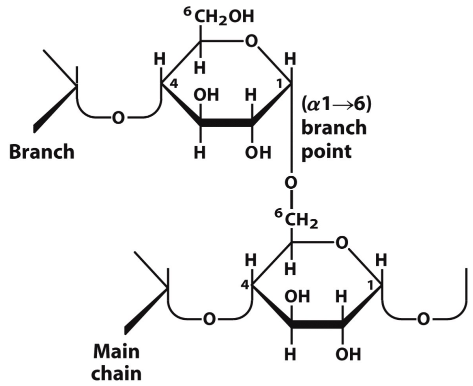

Figure 7-14b
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Starch

- Starch is a mixture of two homopolysaccharides of glucose
  - Amylose is unbranched polymer of ($\alpha 1 \rightarrow 4$) linked residues
  - Amylopectin is branched like glycogen but the branch-points with
    ($\alpha 1 \rightarrow 6$) linkers occur every 24-30 residues
  - Molecular weight of amylopectin is up to 200 million
- Starch is the main storage homopolysaccharide in plants

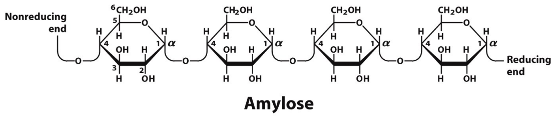

Figure 7-14a
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Metabolism of Glycogen and Starch

- Glycogen and starch often form granules in cells
- Granules contain enzymes that synthesize and degrade these polymers
- Glycogen and amylopectin have one reducing end but many non-reducing ends
- Enzymatic processing occurs simultaneously in many non-reducing ends

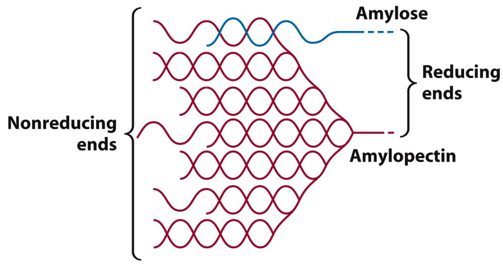

Figure 7-14c
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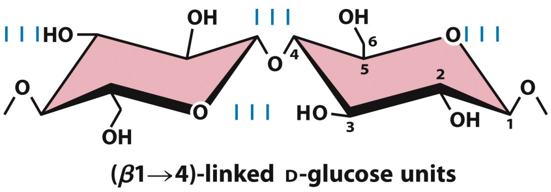
Cellulose

- Cellulose is a branched homopolysaccharide of glucose
  - Glucose monomers form (β1 → 4) linked chains
  - Hydrogen bonds form between adjacent monomers
  - Additional H-bonds between chains
  - Structure is now tough and water-insoluble
  - Most abundant polysaccharide in nature
  - Cotton is nearly pure fibrous cellulose



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Cellulose Metabolism

- The fibrous structure, and water-insolubility makes cellulose a difficult substrate to act on
- Fungi, bacteria, and protozoa secrete cellulase, which allows them to use wood as source of glucose
- Most animals cannot use cellulose as a fuel source because they lack the enzyme to hydrolyze (β1 →4) linkages
- Ruminants and termites live symbiotically with a microorganisms that produces cellulase
- Cellulases hold promise in the fermentation of biomass into biofuels

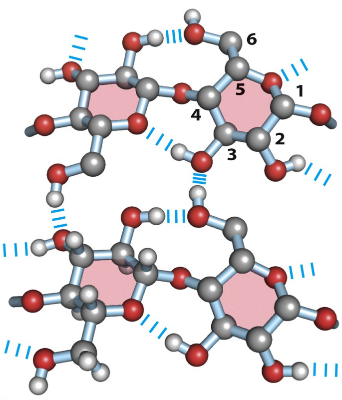

Figure 7-15b
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Figure 7-16
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Do carbohydrates have fixed (or native) structures?

- Think of protein folding problem, and how native protein structure related to its energy status.
- How protein structure is stabilized?
- How carbohydrate structure is stabilized?

Chitin

- Chitin is a linear homopolysaccharide of N-acetylglucosamine
  - N-acetylglucosamine monomers form (β1 → 4) linked chains
  - Forms extended fibers that are similar to those of cellulose
  - Hard, insoluble, cannot be digested by vertebrates
  - Structure is now tough but flexible, and water-insoluble
  - Found in cell walls in mushrooms, and in exoskeletons of insects, spiders, crabs, and other arthropods

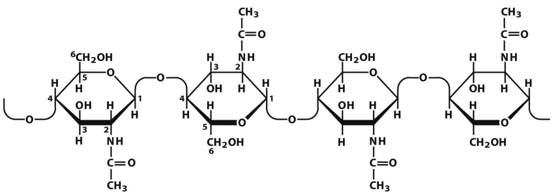

Figure 7-17a
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Figure 7-17b
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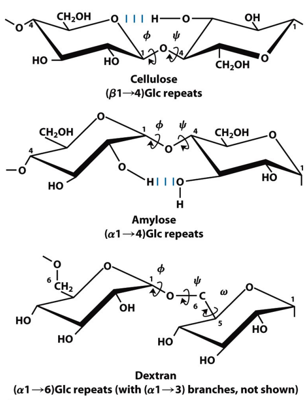

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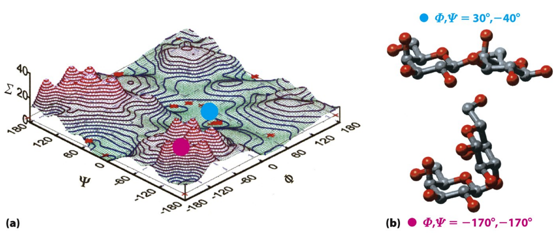

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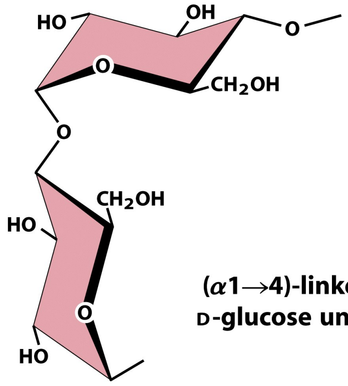

(α1→4)-linked
D-glucose units

Figure 7-20a
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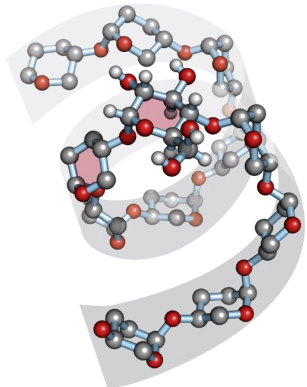

Figure 7-20b
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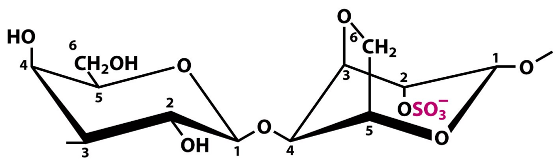
Agar and Agarose

- Agar is a complex mixture of hetereopolysaccharides containing modified galactose units
- Serves as a component of cell wall in some seaweeds
- Agarose is one component of agar:
- Agar solutions form gels that are commonly used in the laboratory as a surface for growing bacteria
- Agarose solutions form gels that are commonly used in the laboratory for separation DNA by electrophoresis



Agarose
3)D-Gal(β1 →4)3,6-anhydro-L-Gal2S(α1 repeating units)

Figure 7-21
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Glycosaminoglycans

- Linear polymers of repeating disaccharide units
- One monomer is either
  - N-acetyl-glucosamine or
  - N-acetyl-galactosamine
- Negatively charged
  - Uronic acids (C6 oxidation)
  - Sulfate esters
- Extended hydrated molecule
  - Minimizes charge repulsion
- Forms meshwork with fibrous proteins to form extracellular matrix
  - Connective tissue
  - Lubrication of joints

How monosaccharides are linked in polysaccharide makes big difference.

Anomer makes difference!

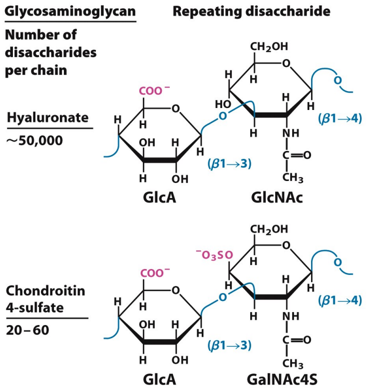

Figure 7-22 part 1a
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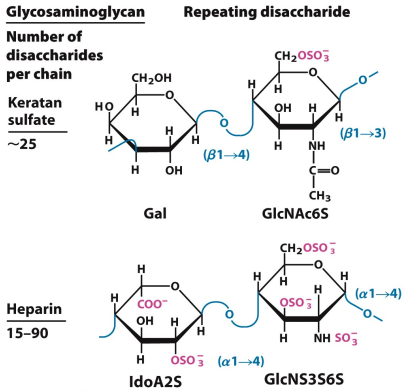

Figure 7-22 part 1b
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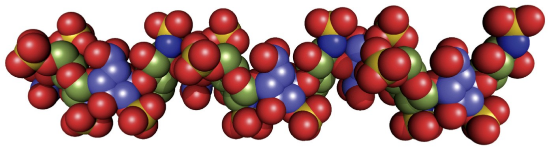
Heparin and Heparan Sulfate

- Heparin is linear polymer, 3 – 40 kDa
- Heparan sulfate is heparin-like polysaccharide but attached to proteins
- Highest negative charge density biomolecules
- Prevent blood clotting by activating protease inhibitor antithrombin
- Binding to various cells regulates development and formation of blood vessels
- Can also bind to viruses and bacteria and decrease their virulence



Heparin segment

Figure 7-22 part 2
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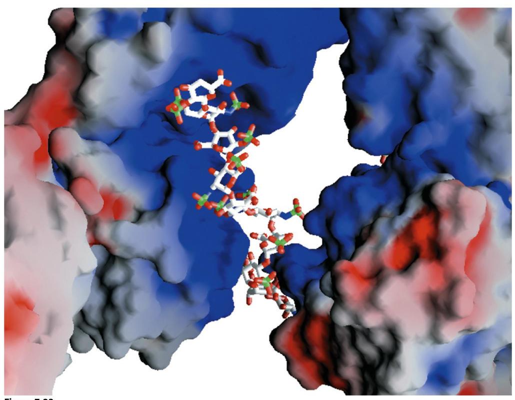

Figure 7-23
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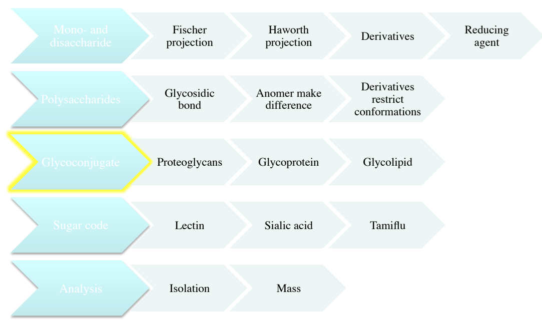

Glycoconjugates: Proteoglycans

- Sulfated glucoseaminoglycans attached to a large rod-shaped protein in cell membrane
  - Syndecans: protein has a single transmembrane domain
  - Glypicans: protein is anchored to a lipid membrane
  - Interact with a variety of receptors from neighboring cells and regulate cell growth

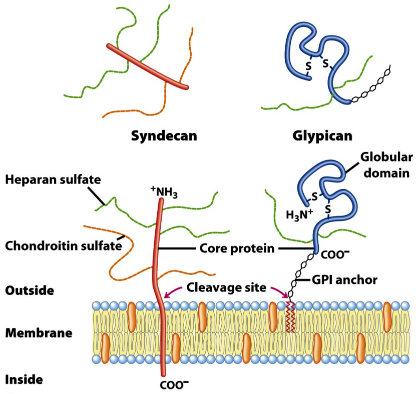

Figure 7-25a
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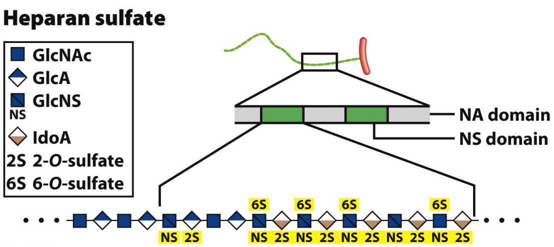

Figure 7-25b
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Proteoglycans

- Different glycosaminoglycans are linked to the core protein
- Linkage from anomeric carbon of xylose to serine hydroxyl
- Our tissues have many different core proteins; aggrecan is the best studied

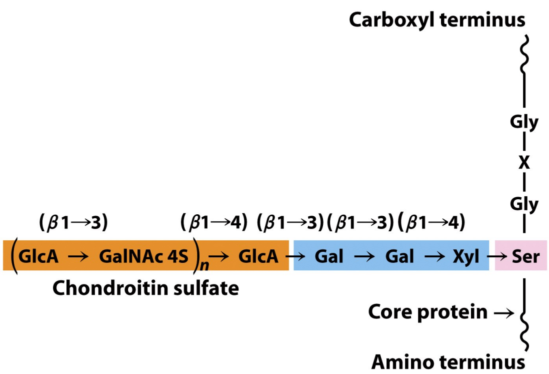

Figure 7-24
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Proteoglycan Aggregates

- Hyaluronan and aggrecan form huge ($M_r > 2•10^8$) non-covalent aggregates
- Hold lots of water (1000 X its weight); provides lubrication
- Very low friction material
- Covers joint surfaces: articular cartilage
  - Reduced friction
  - Load balancing

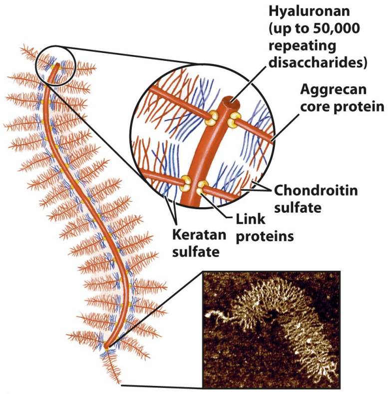

Figure 7-27
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Extracellular Matrix (ECM)

- Material outside the cell
- Strength, elasticity, and physical barrier in tissues
- Main components:
  - Proteoglycan aggregates
  - Collagen fibers
  - Elastin (a fibrous protein)
- ECM is a barrier for tumor cells seeking to invade new tissues
  - Some tumor cells secrete heparinase that degrades ECM

Interaction of the Cells with ECM

- Some integral membrane proteins are proteoglycans
  - Syndecans
- Other integral membrane proteins are receptors for extracellular proteoglycans
  - Integrins
- These proteins link cellular cytoskeleton to the ECM and transmit signals into the cell to regulate
  - Cell growth
  - Cell mobility
  - Apoptosis
  - Wound healing

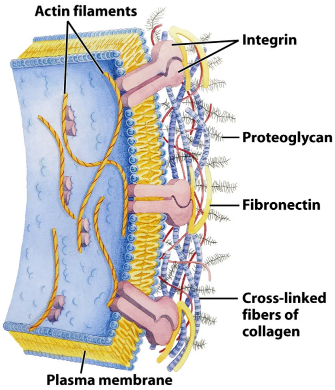

Figure 7-28
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Glycoconjugates: Glycoprotein

- A protein with small oligosaccharides attached
  - Carbohydrate attached via its anomeric carbon
  - About half of mammalian proteins are glycoproteins
  - Carbohydrates play role in protein-protein recognition
  - Only some bacteria glycosylate few of their proteins
  - Viral proteins heavily glycosylated; helps evade the immune system

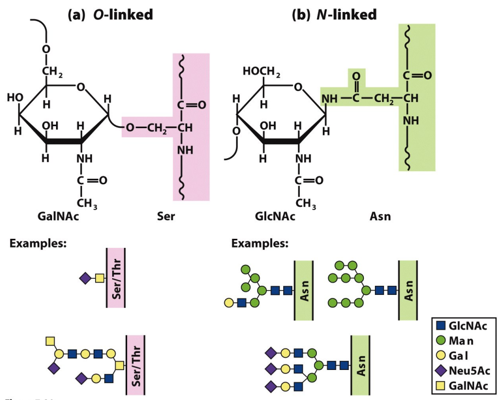

Figure 7-29
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Glycoconjugates: Glycolipids

- A lipid with covalently bound oligosaccharide
  - Parts of plant and animal cell membranes
  - In vertebrates, ganglioside carbohydrate composition determines blood groups
  - In gram-negative bacteria, lipopolysaccharides cover the peptidoglycan layer

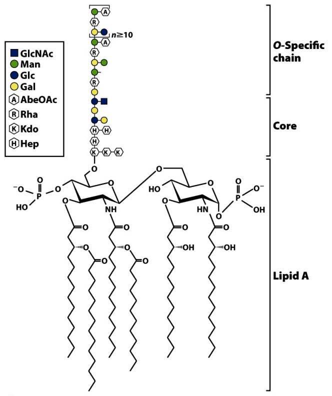

Figure 7-30
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Mono- and disaccharide	Fischer projection	Haworth projection	Derivatives	Reducing agent
Polysaccharides	Glycosidic bond	Anomer make difference	Derivatives restrict conformations	
Glycoconjugate	Proteoglycans	Glycoprotein	Glycolipid	
Sugar code	Lectin	Sialic acid	Tamiflu	
Analysis	Isolation	Mass		

TABLE 7–3 Some Lectins and the Oligosaccharide Ligands They Bind

Lectin source and lectin	Abbreviation	Ligand(s)
Plant		
Concanavalin A	ConA	Manαl—OCH_3
Griffonia simplicifolia lectin 4	GS4	Lewis b (Le^b) tetrasaccharide
Wheat germ agglutinin	WGA	Neu5Ac(α2→3)Gal(β1→4)Glc GlcNAc(β1→4)GlcNAc
Ricin		Gal(β1→4)Glc
Animal		
Galectin-1		Gal(β1→4)Glc
Mannose-binding protein A	MBP-A	High-mannose octasaccharide
Viral		
Influenza virus hemagglutinin	HA	Neu5Ac(α2→6)Gal(β1→4)Glc
Polyoma virus protein 1	VP1	Neu5Ac(α2→3)Gal(β1→4)Glc
Bacterial		
Enterotoxin	LT	Gal
Cholera toxin	CT	GM1 pentasaccharide

Source: Weiss, W.I. & Drickamer, K. (1996) Structural basis of lectin-carbohydrate recognition. *Annu. Rev. Biochem.* **65**, 441–473.

Table 7-3
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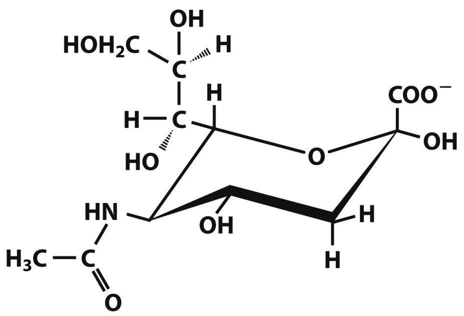

***N*-Acetylneuraminic acid (Neu5Ac)**
(a sialic acid)

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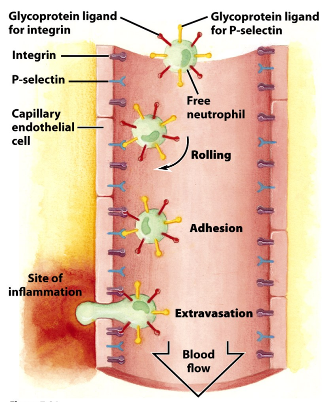

Figure 7-31
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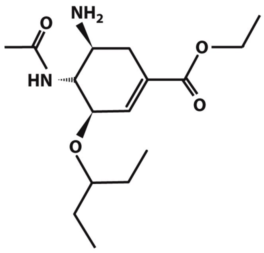
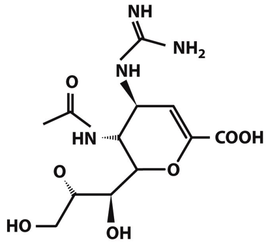


Oseltamivir (Tamiflu)



Zanamivir (Relenza)

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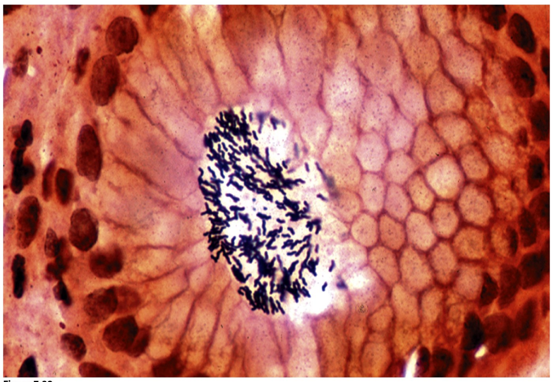

Figure 7-32
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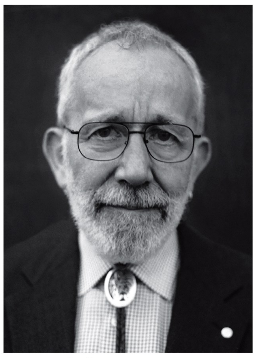
Barry J. Marshall



J. Robin Warren

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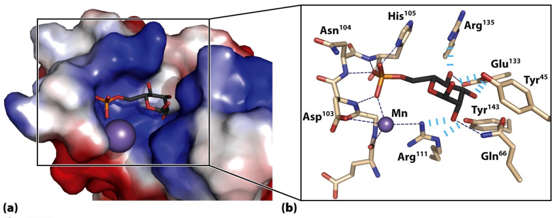

Figure 7-33
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Oligosaccharides in Recognition

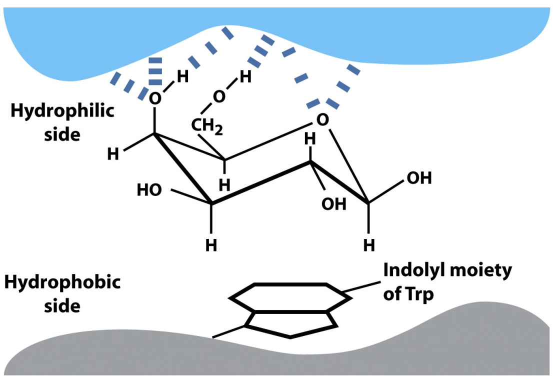

Figure 7-34
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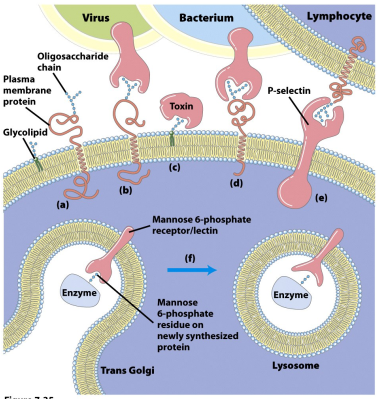

Figure 7-35
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- Mono- and disaccharide: Fischer projection; Haworth projection; Derivatives; Reducing agent
- Polysaccharides: Glycosidic bond; Anomer make difference; Derivatives restrict conformations
- Glycoconjugate: Proteoglycans; Glycoprotein; Glycolipid
- Sugar code: Lectin; Sialic acid; Tamiflu
- Analysis: Isolation; Mass

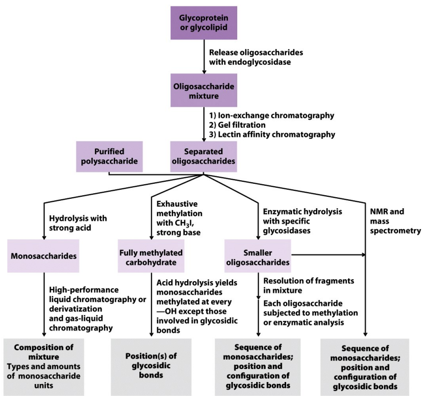

Figure 7-36
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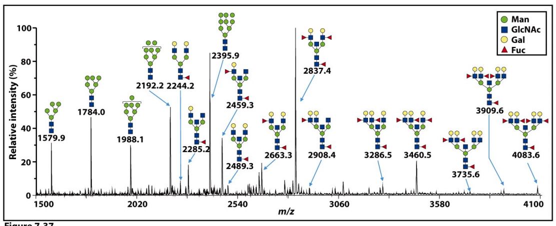

Figure 7-37
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Review of Polysaccharides

TABLE 7–2 Structures and Roles of Some Polysaccharides

Polymer	Type*	Repeating unit†	Size (number of monosaccharide units)	Roles/significance
Starch				Energy storage: in plants
Amylose	Homo-	(α1→4)Glc, linear	50–5,000	
Amylopectin	Homo-	(α1→4)Glc, with (α1→6)Glc branches every 24–30 residues	Up to 10^6	
Glycogen	Homo-	(α1→4)Glc, with (α1→6)Glc branches every 8–12 residues	Up to 50,000	Energy storage: in bacteria and animal cells
Cellulose	Homo-	(β1→4)Glc	Up to 15,000	Structural: in plants, gives rigidity and strength to cell walls
Chitin	Homo-	(β1→4)GlcNAc	Very large	Structural: in insects, spiders, crustaceans, gives rigidity and strength to exoskeletons
Dextran	Homo-	(α1→6)Glc, with (α1→3) branches	Wide range	Structural: in bacteria, extracellular adhesive
Peptidoglycan	Hetero-; peptides attached	4)Mur2Ac(β1→4) GlcNAc(β1	Very large	Structural: in bacteria, gives rigidity and strength to cell envelope
Agarose	Hetero-	3)D-Gal(β1→4)3,6-anhydro-L-Gal(α1	1,000	Structural: in algae, cell wall material
Hyaluronan (a glycosaminoglycan)	Hetero-; acidic	4)GlcA(β1→3) GlcNAc(β1	Up to 100,000	Structural: in vertebrates, extracellular matrix of skin and connective tissue; viscosity and lubrication in joints

*Each polymer is classified as a homopolysaccharide (homo-) or heteropolysaccharide (hetero-).

†The abbreviated names for the peptidoglycan, agarose, and hyaluronan repeating units indicate that the polymer contains repeats of this disaccharide unit. For example, in peptidoglycan, the GlcNAc of one disaccharide unit is (β1→4)-linked to the first residue of the next disaccharide unit.

Table 7-2
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Chapter 7: Summary

In this chapter, we learned about:

- structures of some important monosaccharides
- structures and properties of disaccharides
- structures and biological roles of polysaccharides
- functions of glycosylaminoglycans as structural components of the extracellular matrix
- functions glycoconjugates in regulating a variety of biological functions