

7 Carbohydrates and Glycobiology

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Learning



Carbohydrates

- **carbohydrates** = aldehydes or ketones with at least two hydroxyl groups, or substances that yield such compounds on hydrolysis
- many carbohydrates have the empirical formula $(\text{CH}_2\text{O})_n$

Classes of Carbohydrates

- **monosaccharides** = simple sugars, consist of a single polyhydroxy aldehyde or ketone unit
 - example: D-glucose
- **oligosaccharides** = short chains of monosaccharide units, or residues, joined by glycosidic bonds

Classes of Carbohydrates, Continued

- **disaccharides** = oligosaccharides with two monosaccharide units
 - example: sucrose (D-glucose and D-fructose)
- **polysaccharides** = sugar polymers with 10+ monosaccharide units
 - examples: cellulose (linear), glycogen (branched)

Principle 1 (1 of 4)

Carbohydrates can have multiple chiral carbons; the configuration of groups around each carbon atom determines how the compound interacts with other biomolecules. As we saw for L-amino acids in proteins, with rare exceptions, biological evolution selected one stereochemical series (D-series) for sugars.

Principle 2 (1 of 3)

Monomeric subunits, monosaccharides, serve as the building blocks of large carbohydrate polymers. The specific sugar, the way the units are linked, and whether the polymer is branched determine its properties and thus its function.

P3 Principle 3 (1 of 2)

Storage of low molecular weight metabolites in polymeric form avoids the very high osmolarity that would result from storing them as individual monomers. If the glucose in liver glycogen were monomeric, the glucose concentration in liver would be so high that cells would swell and lyse from the entry of water by osmosis.

Principle 4 (1 of 2)

The sequences of complex polysaccharides are determined by the intrinsic properties of the biosynthetic enzymes that add each monomeric unit to the growing polymer. This is in contrast with DNA, RNA, and proteins, which are synthesized on templates that direct their sequence.

P5 Principle 5 (1 of 6)

Polysaccharides assume three-dimensional structures with the lowest-energy conformations, determined by covalent bonds, hydrogen bonds, charge interactions, and steric factors. Starch folds into a helical structure stabilized by internal hydrogen bonds; cellulose assumes an extended structure in which intermolecular hydrogen bonds are more important.

Principle 6 (1 of 4)

Molecular complementarity is central to function.
The recognition of oligosaccharides by sugar-binding proteins (lectins) results from a perfect fit between lectin and ligand.



Principle 7 (1 of 3)

An almost infinite variety of discrete structures can be built from a small number of monomeric subunits. Even short polymers, when arranged in different sequences, joined through different linkages, and branched to specific degrees, present unique faces recognized by their molecular partners.

7.1 Monosaccharides and Disaccharides

Stereoisomerism in Sugars

- sugar stereoisomers arise because many of the carbon atoms to which the hydroxyl groups are attached are chiral centers
- enzymes that act on sugars are stereospecific

Principle 1 (2 of 4)

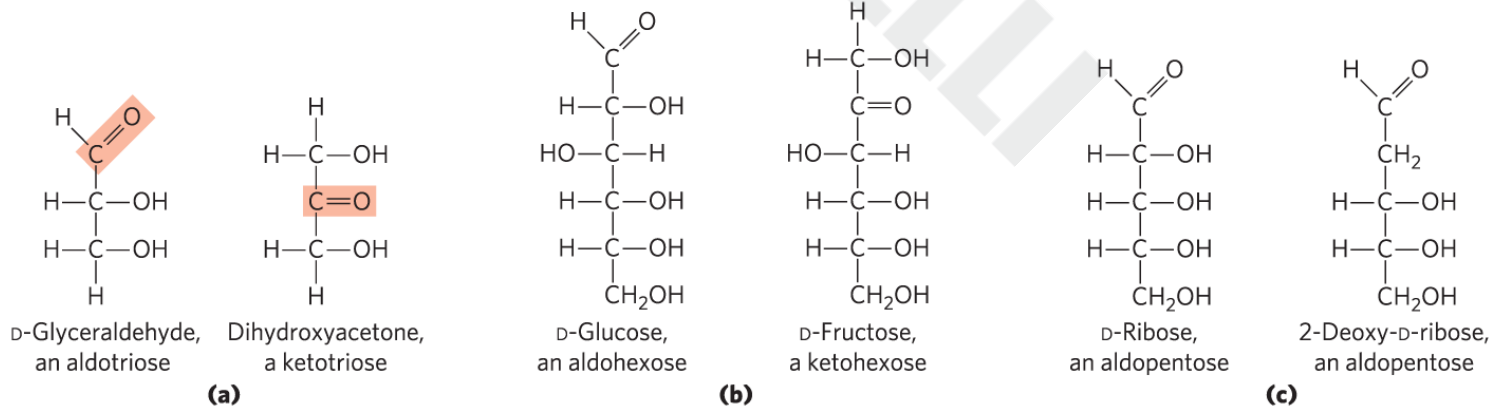
Carbohydrates can have multiple chiral carbons; the configuration of groups around each carbon atom determines how the compound interacts with other biomolecules. As we saw for L-amino acids in proteins, with rare exceptions, biological evolution selected one stereochemical series (D-series) for sugars.

The Two Families of Monosaccharides Are Aldoses and Ketoses

- backbones of monosaccharides:
 - unbranched carbon chains with single bonds linking all carbon atoms
 - one of the carbon atoms is double-bonded to an oxygen atom to form a carbonyl group
 - other carbon atoms are bonded to a hydroxyl group

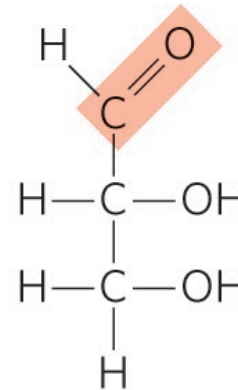
Aldoses and Ketoses

- **aldose** = carbonyl group is at an end of the carbon chain (in an aldehyde group)
- **ketose** = carbonyl group is at any other position (in a ketone group)

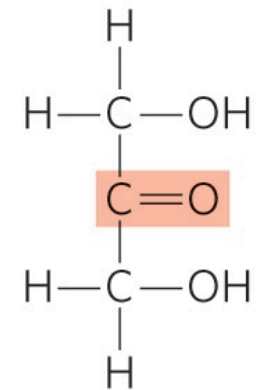


Trioses

- trioses = simplest monosaccharides, three carbon backbone



D-Glyceraldehyde,
an aldotriose



Dihydroxyacetone,
a ketotriose

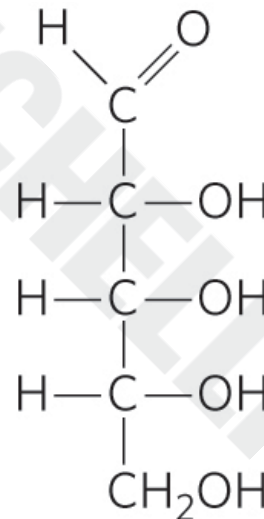
(a)

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Tetroses and Pentoses

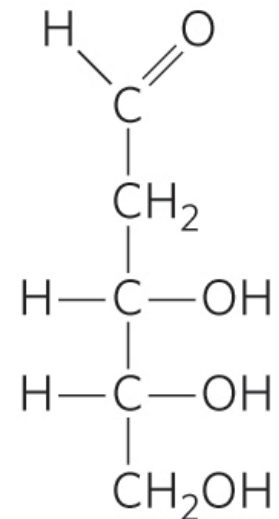
- tetroses = four carbon backbone
- pentoses = five carbon backbone

component
of RNA



D-Ribose,
an aldopentose

component
of DNA



2-Deoxy-D-ribose,
an aldopentose

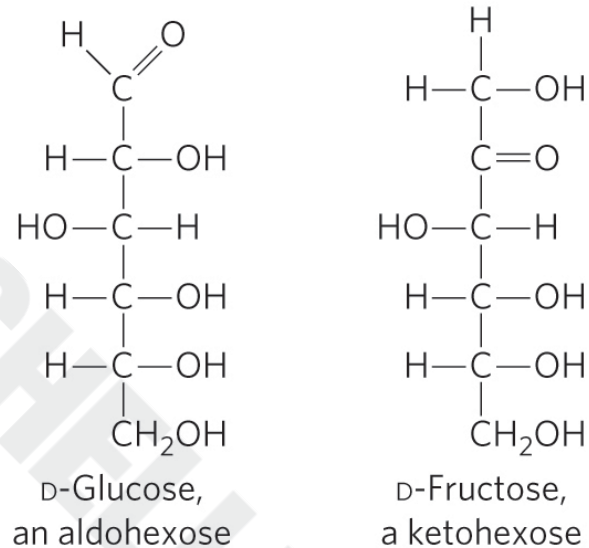
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Hexoses and Heptoses

- hexoses = six carbon backbone
- heptoses = seven carbon backbone

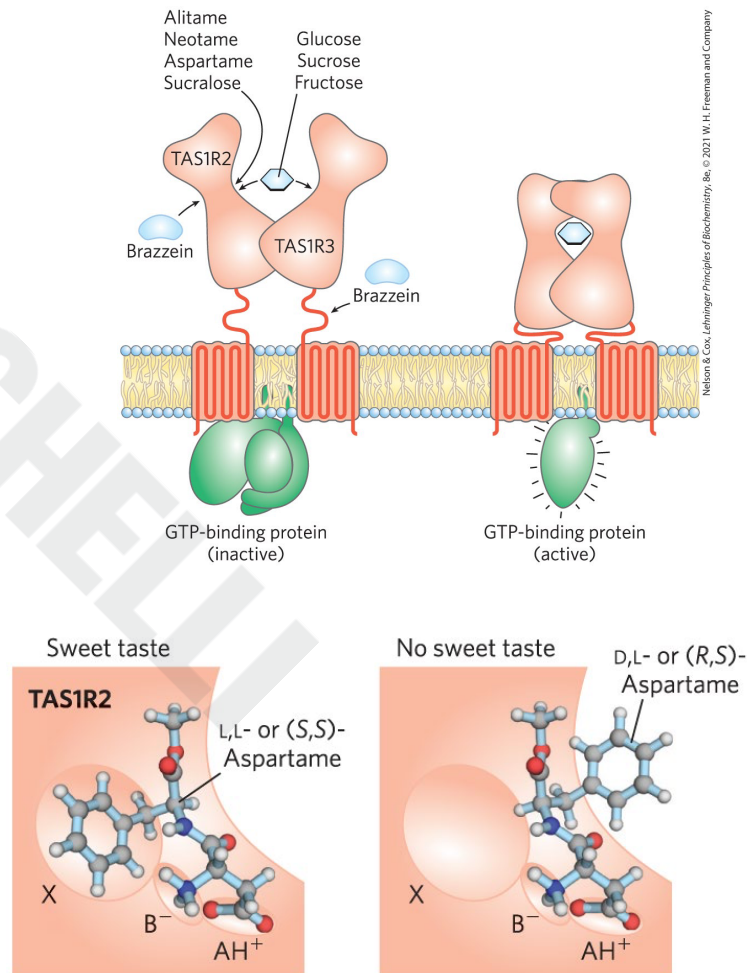


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What Makes Sugar Sweet?

- *TAS1R2* and *TAS1R3* encode sweet-taste receptors
- binding of a compatible molecule generates a “sweet” electrical signal in the brain
 - requires a steric match



Principle 1 (3 of 4)

Carbohydrates can have multiple chiral carbons; the configuration of groups around each carbon atom determines how the compound interacts with other biomolecules. As we saw for L-amino acids in proteins, with rare exceptions, biological evolution selected one stereochemical series (D-series) for sugars.

Monosaccharides Have Asymmetric Centers

- all monosaccharides (except dihydroxyacetone) contain 1+ chiral carbon atom
 - occur in optically active isomeric forms
- **enantiomers** = two different optical isomers that are mirror images
- in general, a molecule with n chiral centers can have 2^n stereoisomers

Fischer Projection Formulas

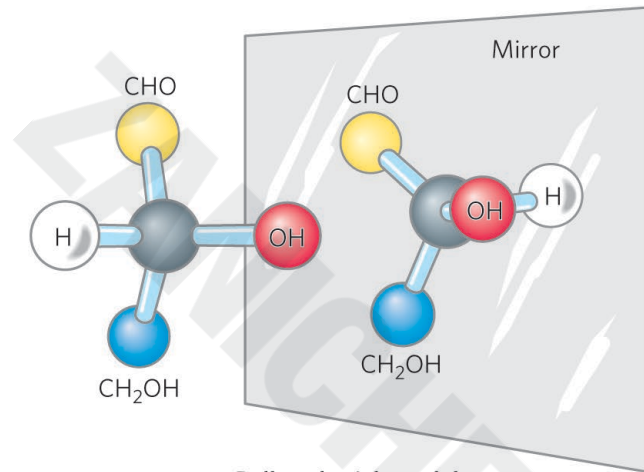
- used to represent three-dimensional sugar structures on paper
- bonds drawn horizontally indicate bonds that project out of the plane of the paper
- bonds drawn vertically project behind the plane of the paper



Fischer projection formulas

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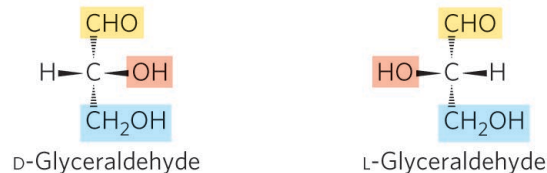
Enantiomers of Glyceraldehyde



Ball-and-stick models



Fischer projection formulas



Perspective formulas

Principle 1 (4 of 4)

Carbohydrates can have multiple chiral carbons; the configuration of groups around each carbon atom determines how the compound interacts with other biomolecules. As we saw for L-amino acids in proteins, with rare exceptions, biological evolution selected one stereochemical series (D-series) for sugars.

D Isomers and L Isomers

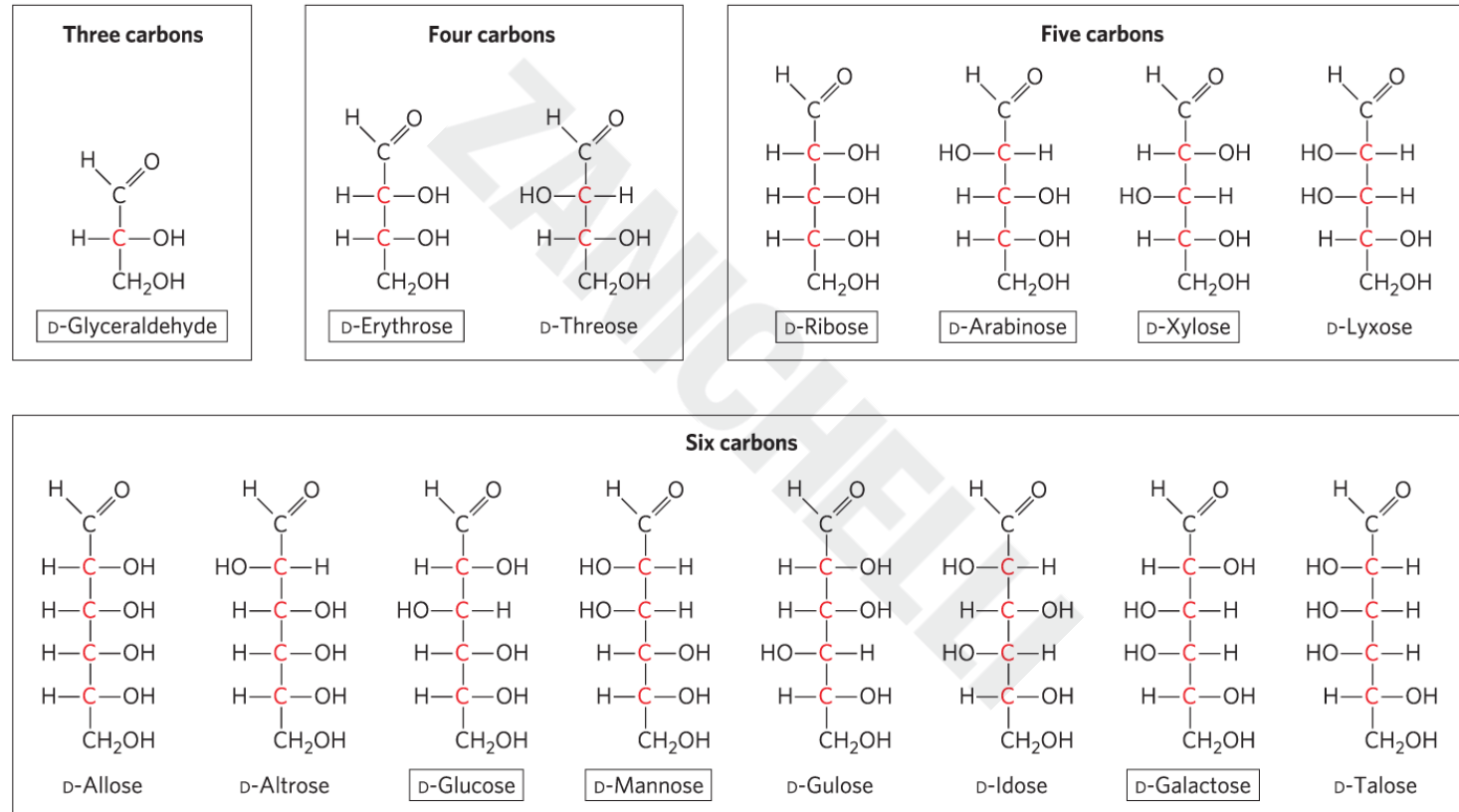
- reference carbon = chiral center *most distant* from the carbonyl carbon
- two groups of stereoisomers:
 - D isomers = configuration at reference carbon is the same as D-glyceraldehyde
 - on the right (*dextro*) in a projection formula
 - most hexoses of living organisms
 - L isomers = configuration at reference carbon is the same as L-glyceraldehyde
 - on the left (*levo*) in a projection formula

Numbering Carbons of a Sugar

- carbons are numbered beginning at the end of the chain near the carbonyl group

D-Aldoses

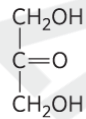
(a) D-Aldoses



D-Ketoses

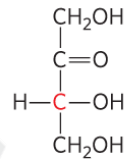
(b) D-Ketoses

Three carbons



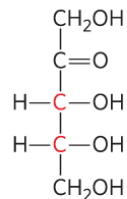
Dihydroxyacetone

Four carbons

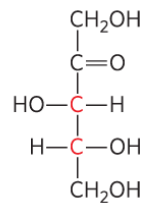


D-Erythrulose

Five carbons

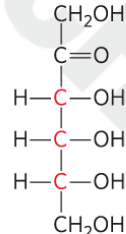


D-Ribulose

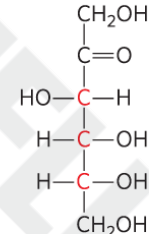


D-Xylulose

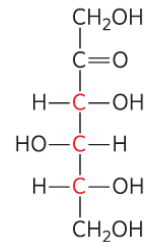
Six carbons



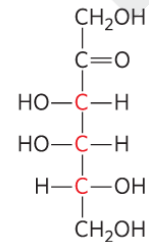
D-Psicose



D-Fructose



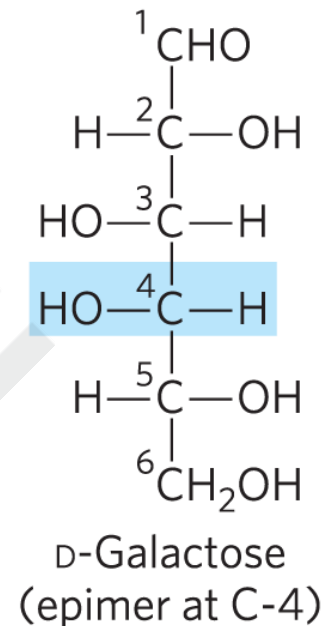
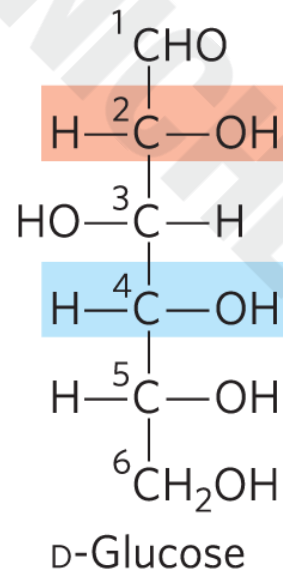
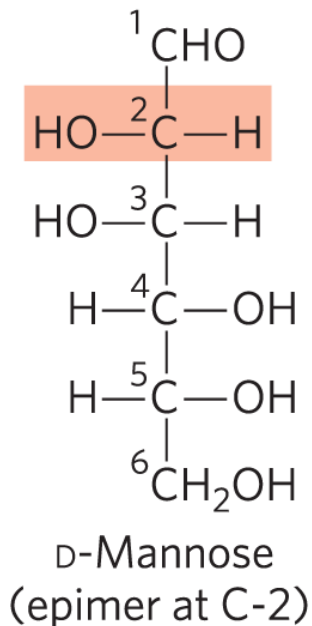
D-Sorbose



D-Tagatose

Epimers

- epimers** = two sugars that differ only in the configuration around one carbon atom



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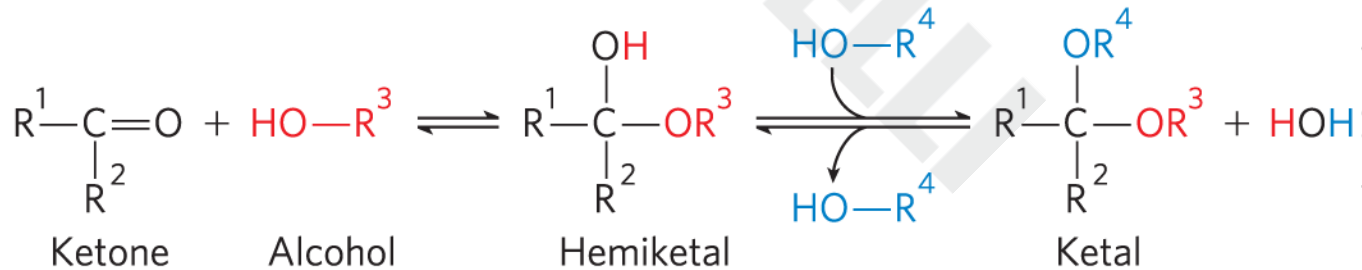
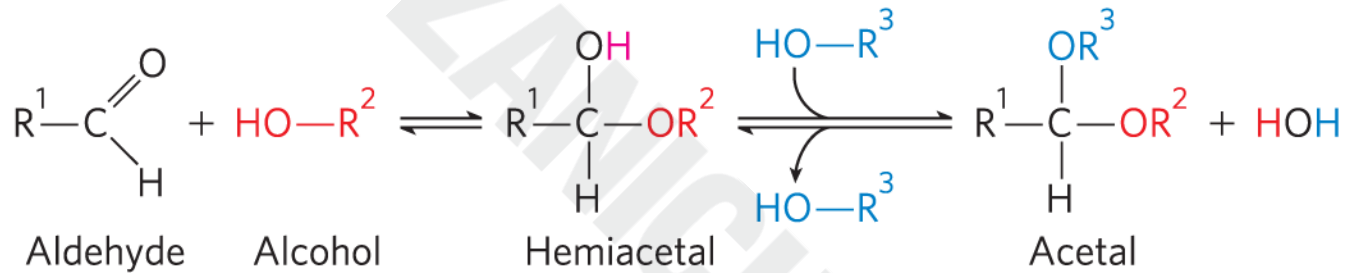
The Common Monosaccharides Have Cyclic Structures

- in aqueous solution, aldotetroses and all monosaccharides with 5+ backbone carbon atoms occur as cyclic structures
 - covalent bond between the carbonyl group and the oxygen of a hydroxyl group

Hemiacetals and Hemiketals

- **hemiacetals** or **hemiketals** = derivatives formed by a general reaction between alcohols and aldehydes or ketones
 - product of the first alcohol molecule addition
 - a five- or six-membered ring forms if the —OH and carbonyl groups are on the same molecule
- **acetal** or **ketal** = product of the second alcohol molecule addition
 - forms a glycosidic bond

Formation of Hemiacetals and Hemiketals



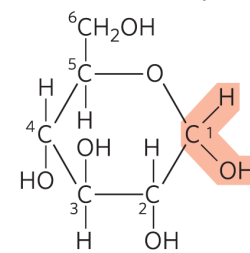
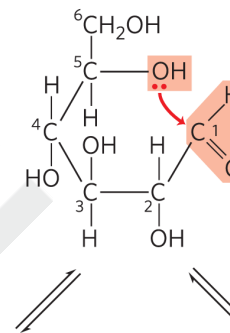
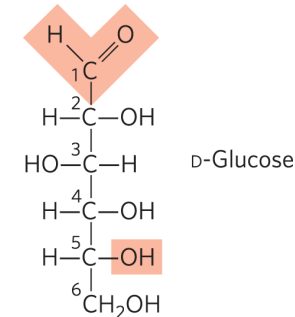
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α and β Stereoisomeric Configurations

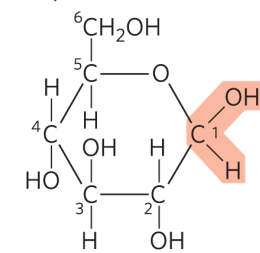
- reaction with the first alcohol molecule creates an additional chiral center (the carbonyl carbon)
- produces either of two stereoisomeric configurations: α and β
- **anomers** = isomeric forms of monosaccharides that differ only in their configuration about the hemiacetal or hemiketal carbon atom
- **anomeric carbon** = the carbonyl carbon atom

Formation of the Two Cyclic Forms of D-Glucose

- reaction between the aldehyde group at C-1 and the hydroxyl group at C-5 forms a hemiacetal linkage
- **mutarotation** = the interconversion of α and β anomers



α -D-Glucopyranose

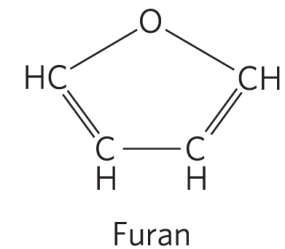
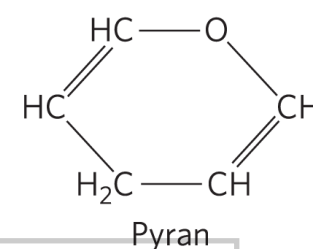
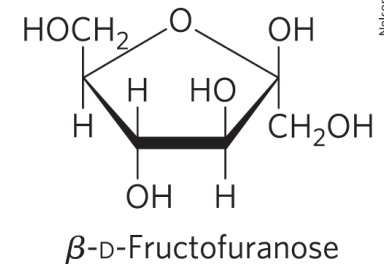
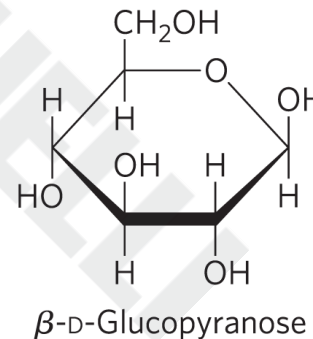
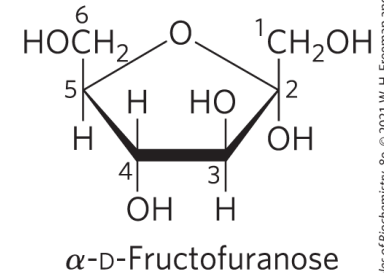
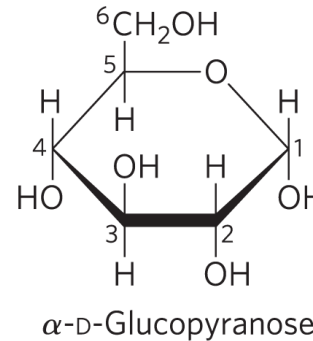


β -D-Glucopyranose

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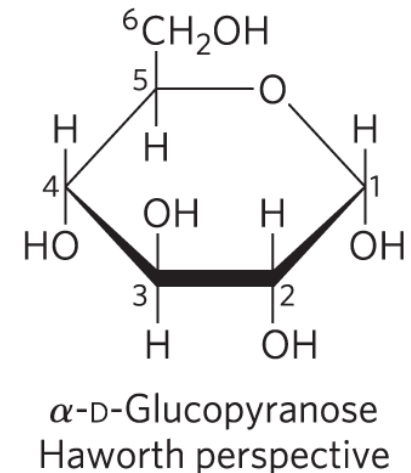
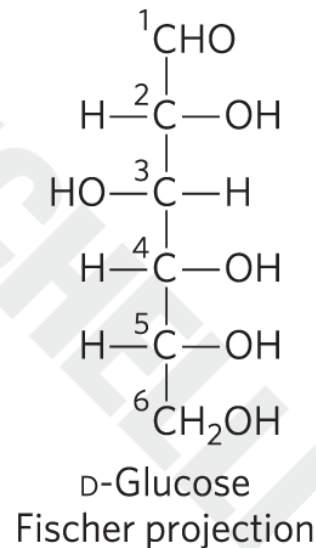
Pyranoses and Furanoses

- **pyranoses** = six-membered ring compounds
 - form when the hydroxyl group at C-6 reacts with the keto group at C-2
- **furanoses** = five-membered ring compounds
 - form when the hydroxyl group at C-5 reacts with the keto group at C-2



Haworth Perspective Formulas

- **Haworth perspective formulas** = more accurate representation of cyclic sugar structure than Fischer projections
 - six-membered ring is tilted to make its plane almost perpendicular to that of the paper
 - bonds closest to the reader are drawn thicker than those farther away



Converting D-Hexose Fischer Projections to Haworth Perspective Formulas

- step 1: draw the six-membered ring (five carbons, and one oxygen at the upper right)
- step 2: number the carbons in a clockwise direction beginning with the anomeric carbon
- step 3: place the hydroxyl groups
 - hydroxyl groups on the right in a Fischer projection are placed pointing down and those on the left are placed pointing up

Converting D-Hexose Fischer Projections to Haworth Perspective Formulas, Continued

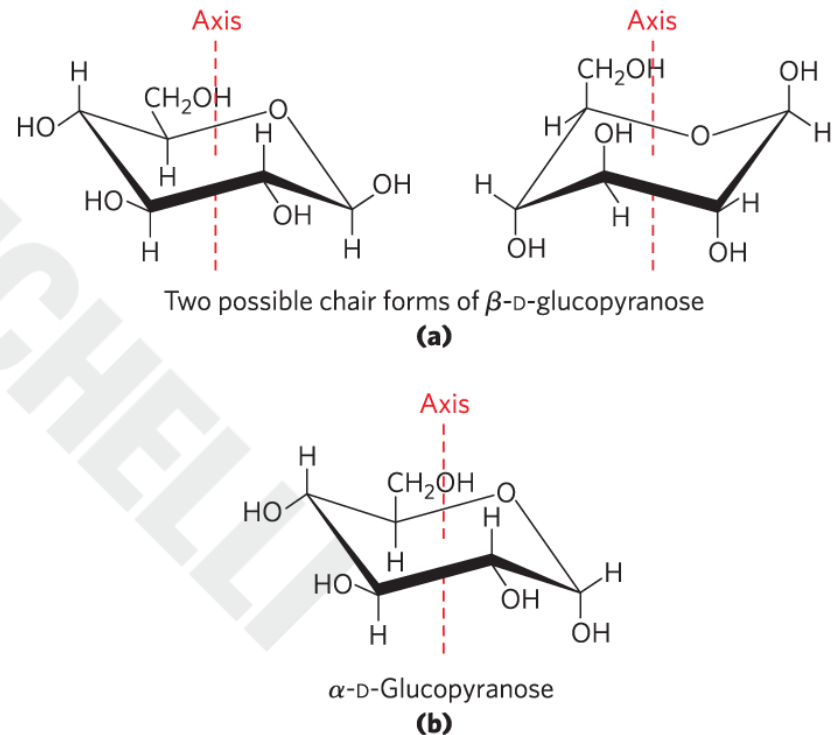
- step 4: place the terminal $\text{—CH}_2\text{OH}$ group
 - projects upward for the D enantiomer, downward for the L enantiomer
- step 5: place the anomeric hydroxyl group
 - for a β structure, the hydroxyl group is placed on the same side of the ring as C-6
 - for an α structure, it is placed on the opposite side

P5 Principle 5 (2 of 6)

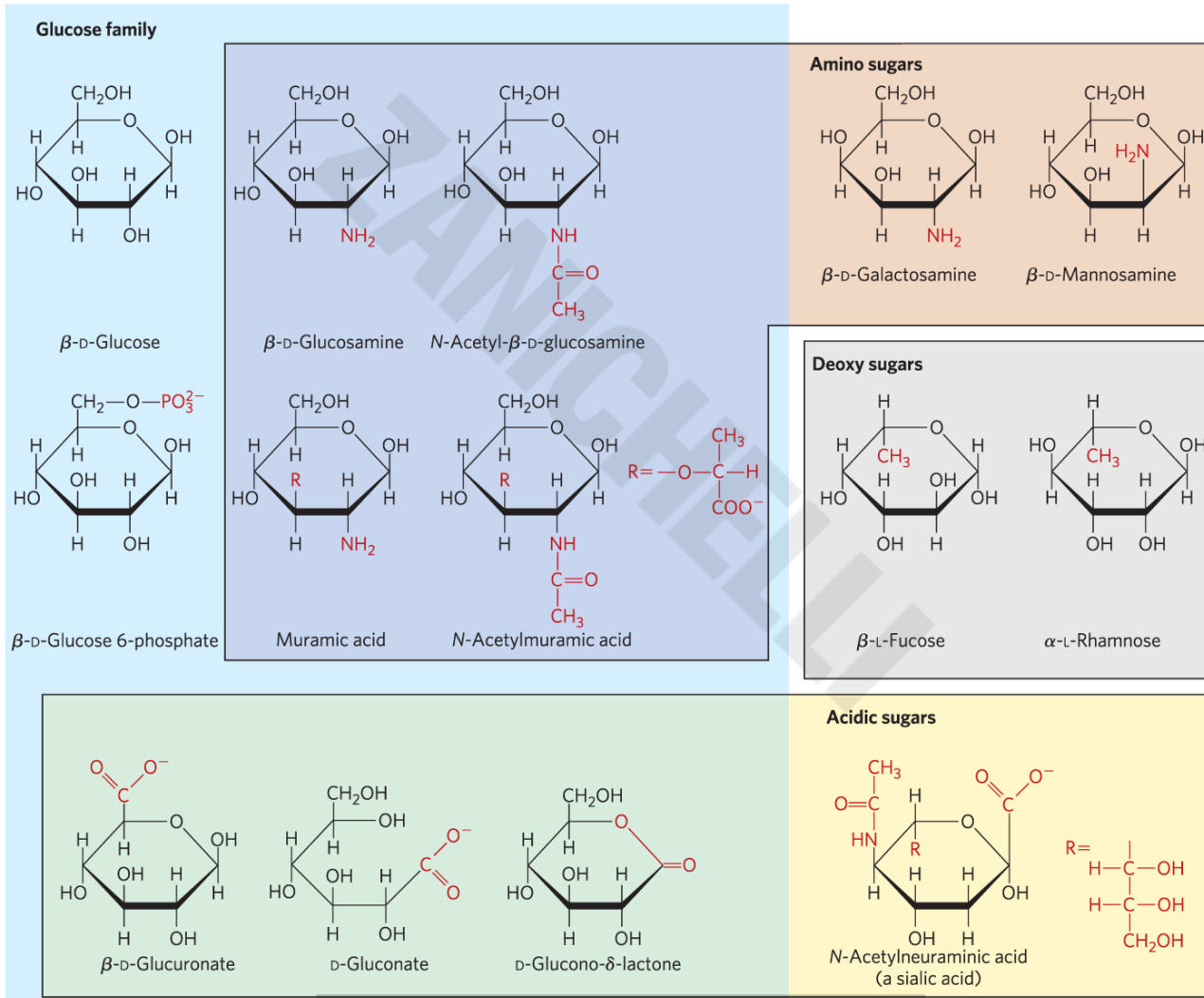
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Conformational Formulas of Pyranoses

- pyranose rings tend to assume either of two “chair” conformations
 - interconvertible without breaking covalent bonds
 - requires energy input



Organisms Contain a Variety of Hexose Derivatives



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Aldonic and Uronic Acids

- **aldonic acids** = form following oxidation of the carbonyl carbon of aldoses
- **uronic acids** = form following oxidation at C-6
- both form stable intramolecular esters called lactones

Phosphorylated Derivatives

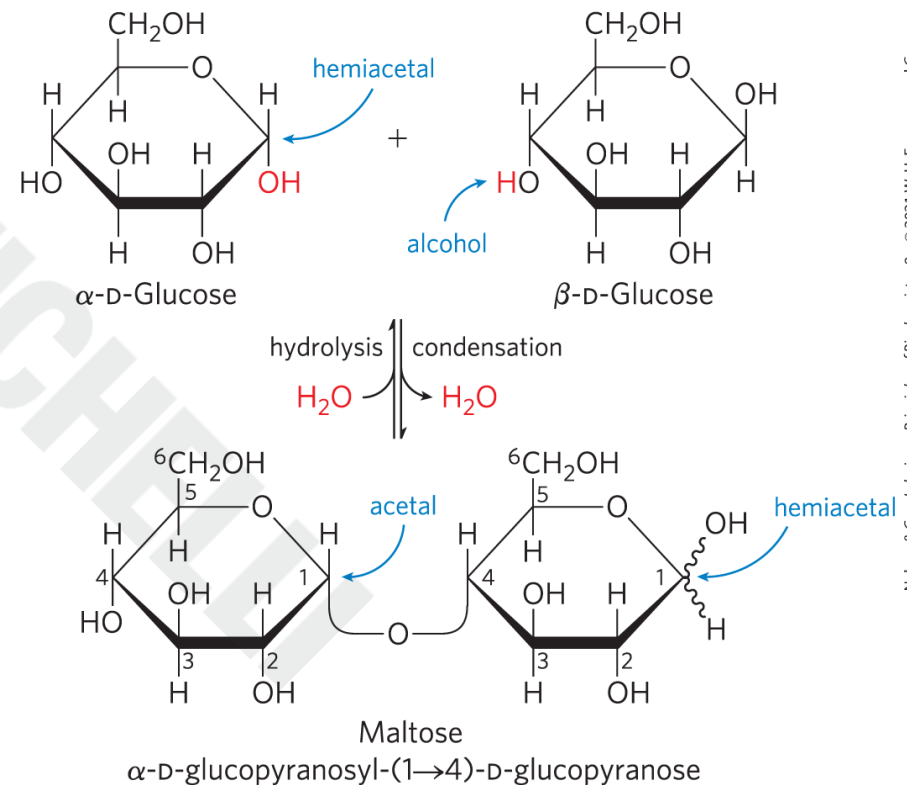
- some sugar intermediates are phosphate esters
 - example: glucose 6-phosphate
- stable at neutral pH and bear a negative charge
- functions to trap sugar inside the cell because most cells do not have membrane transporters for phosphorylated sugars

Sugars That Are, or Can Form, Aldehydes Are Reducing Sugars

- **reducing sugars** = undergo a characteristic redox reaction where free aldehyde groups react with Cu^{2+} under alkaline condition
 - reduction of Cu^{2+} to Cu^+ forms a brick-red precipitate
- ketoses that can tautomerize to form aldehydes are also reducing sugars

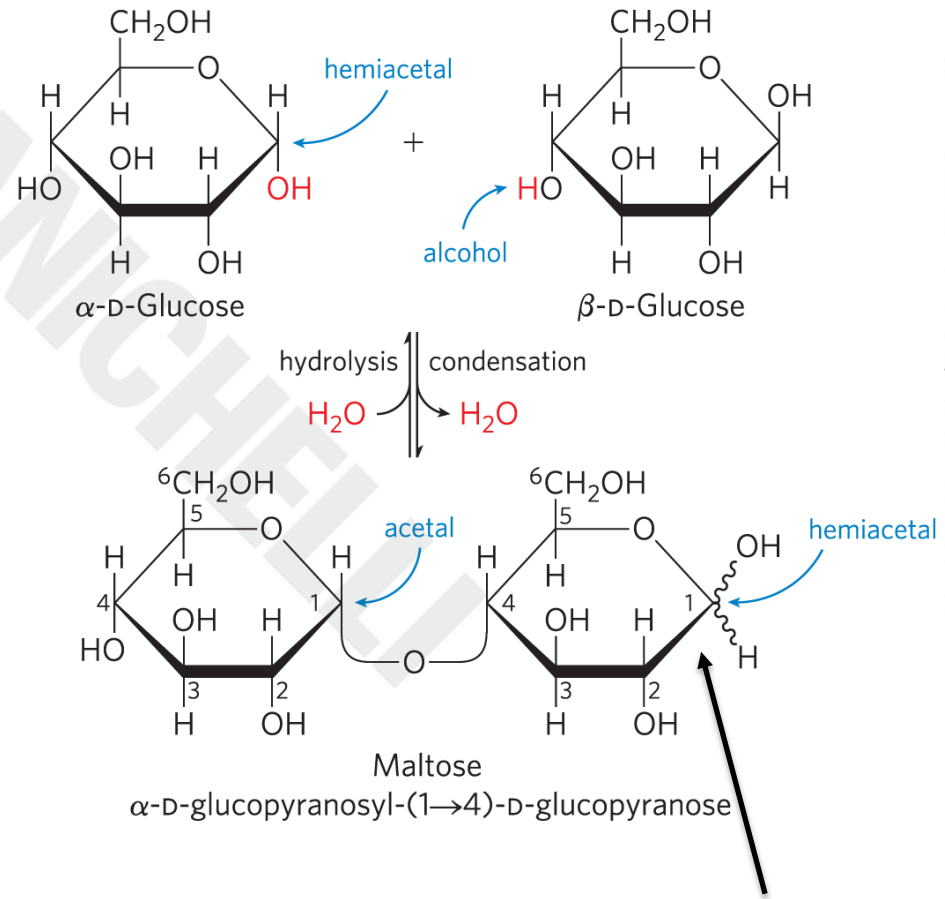
O-Glycosidic Bonds

- **O-glycosidic bond** = covalent linkage joining two monosaccharides
 - formed when a hydroxyl group of one sugar molecule reacts with the anomeric carbon of the other
 - readily hydrolyzed by acid



The Reducing End

- formation of a glycosidic bond renders a sugar nonreducing
- **reducing end** = the end of a disaccharide or polysaccharide chain with a free anomeric carbon



Free anomeric carbon

Naming Reducing Oligosaccharides

- step 1: with the nonreducing end on the left, give the configuration (α or β) at the anomeric carbon joining the first unit to the second
- step 2: name the nonreducing residue using “furano” or “pyrano”
- step 3: indicate in parentheses the two carbon atoms joined by the glycosidic bond, with an arrow connecting the two numbers
- step 4: name the second residue and repeat for additional residues

Symbols and Abbreviations for Monosaccharides and Derivatives

TABLE 7-1

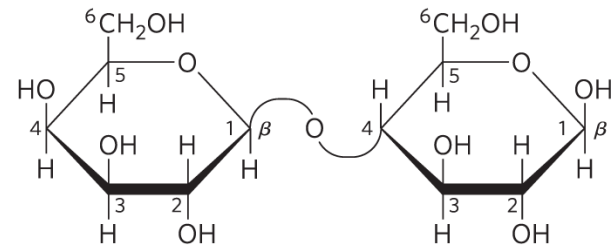
Symbols and Abbreviations for Common Monosaccharides and Some of Their Derivatives

Abequose	Abe	Glucuronic acid	◊ GlcA
Arabinose	Ara	Galactosamine	◻ GalN
Fructose	Fru	Glucosamine	◻ GlcN
Fucose	▲ Fuc	<i>N</i> -Acetylgalactosamine	◻ GalNAc
Galactose	● Gal	<i>N</i> -Acetylglucosamine	■ GlcNAc
Glucose	● Glc	Iduronic acid	◊ IdoA
Mannose	● Man	Muramic acid	Mur
Rhamnose	Rha	<i>N</i> -Acetylmuramic acid	Mur2Ac
Ribose	Rib	<i>N</i> -Acetylneuraminic acid (a sialic acid)	◊ Neu5Ac
Xylose	★ Xyl		

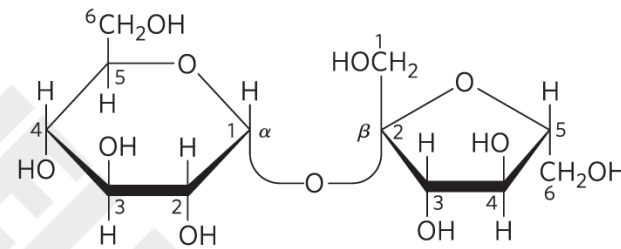
Note: In a commonly used convention, hexoses are represented as circles, *N*-acetylhexosamines as squares, and hexosamines as squares divided diagonally. All sugars with the "gluco" configuration are blue, those with the "galacto" configuration are yellow, and "manno" sugars are green. Other substituents can be added as needed: sulfate (S), phosphate (P), *O*-acetyl (OAc), or *O*-methyl (OMe).

Three Common Disaccharides

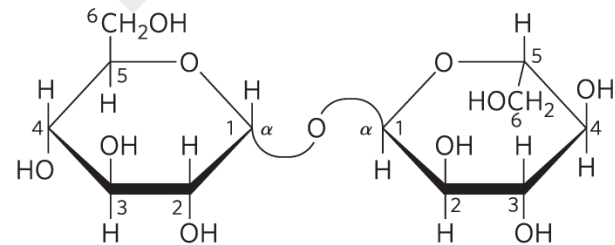
- lactose is a reducing disaccharide
- sucrose and trehalose are nonreducing sugars



Lactose (β form)
 β -D-galactopyranosyl-(1 \rightarrow 4)- β -D-glucopyranose
 Gal(β 1 \rightarrow 4)Glc



Sucrose
 β -D-fructofuranosyl α -D-glucopyranoside
 Fru(2 β \leftrightarrow α 1)Glc \equiv Glc(α 1 \leftrightarrow 2 β)Fru



Trehalose
 α -D-glucopyranosyl α -D-glucopyranoside
 Glc(α 1 \leftrightarrow 1 α)Glc

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7.2 Polysaccharides

Principle 2 (2 of 3)

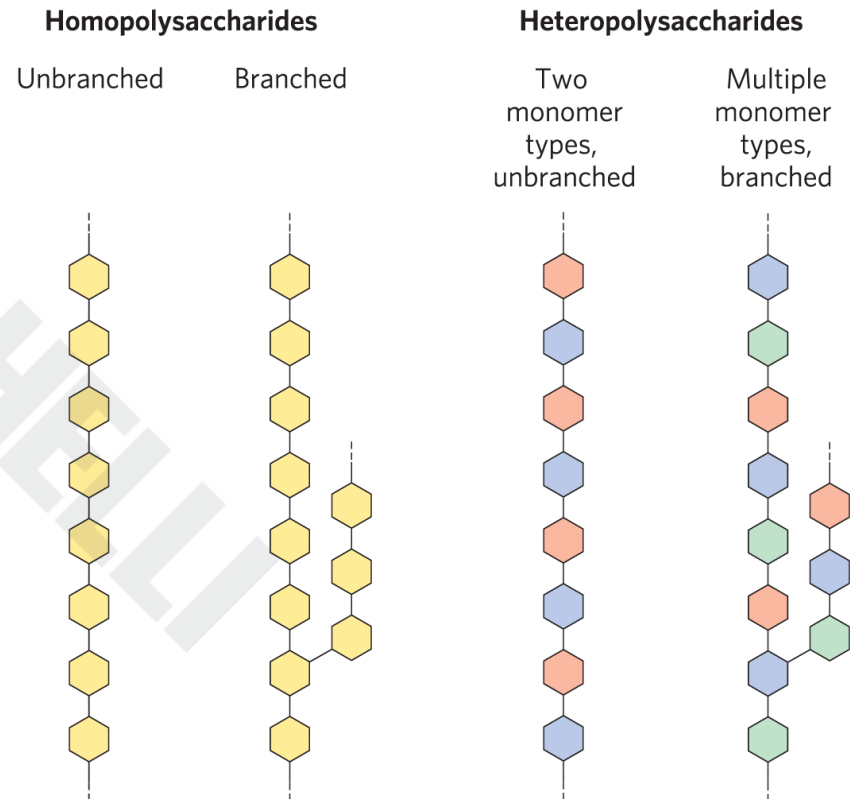
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Polysaccharides

- most carbohydrates in nature occur as polysaccharides ($M_r > 20,000$)
- also called **glycans**

Homopolysaccharides and Heteropolysaccharides

- **homopolysaccharides** = contain only a single monomeric sugar species
 - serve as storage forms and structural elements
- **heteropolysaccharides** = contain 2+ kinds of monomers
 - provide extracellular support



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Principle 4 (2 of 2)

The sequences of complex polysaccharides are determined by the intrinsic properties of the biosynthetic enzymes that add each monomeric unit to the growing polymer. This is in contrast with DNA, RNA, and proteins, which are synthesized on templates that direct their sequence.

Polysaccharides Generally Do Not Have Defined Lengths or Molecular Weights

- this distinction between proteins and polysaccharides is a consequence of the mechanisms of assembly
- there is no template for polysaccharide synthesis
- the program for polysaccharide synthesis is intrinsic to the enzymes that catalyze the polymerization of monomer units

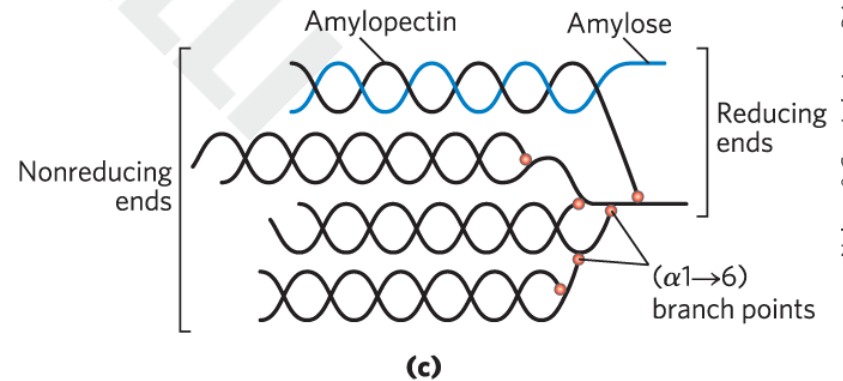
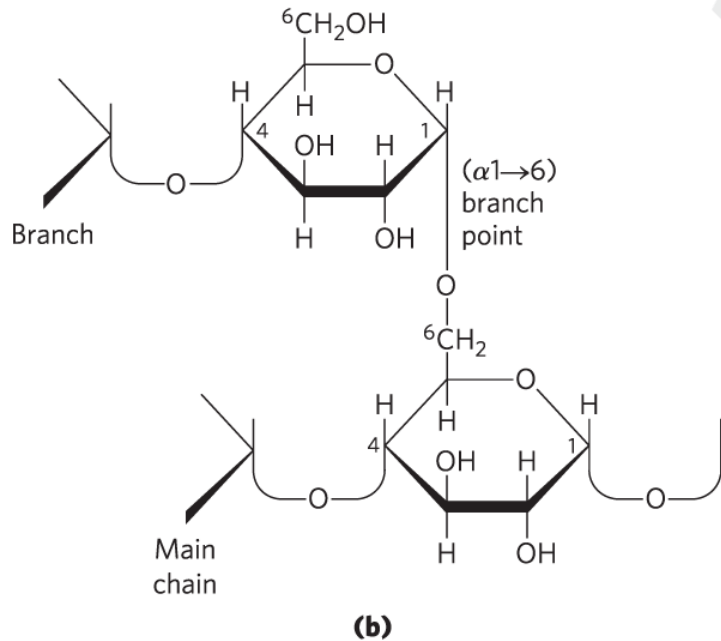
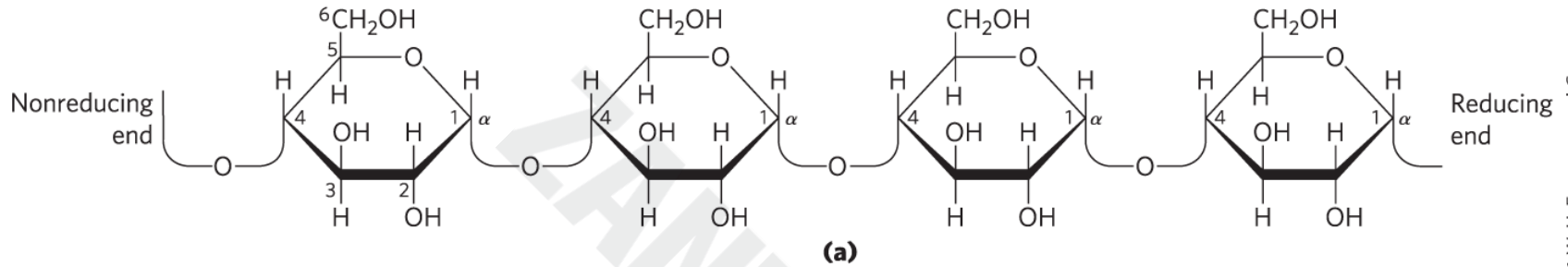
Some Homopolysaccharides Are Storage Forms of Fuel

- storage polysaccharides = starch in plant cells and glycogen in animal cells
- starch and glycogen molecules are heavily hydrated because they have many exposed hydroxyl groups available to hydrogen bond

Starch and Glycogen

- **starch** = contains two types of glucose polymer, amylose and amylopectin
 - amylose = long, unbranched chains of D-glucose residues connected by ($\alpha 1 \rightarrow 4$) linkages
 - amylopectin = larger than amylose with ($\alpha 1 \rightarrow 4$) linkages between glucose residues and highly branched due to ($\alpha 1 \rightarrow 6$) linkages
- **glycogen** = polymer of ($\alpha 1 \rightarrow 4$)-linked glucose subunits, with ($\alpha 1 \rightarrow 6$)-linked branches
 - more extensively branched
 - more compact than starch

Structure of Starch and Glycogen



P3 Principle 3 (2 of 2)

Storage of low molecular weight metabolites in polymeric form avoids the very high osmolarity that would result from storing them as individual monomers. If the glucose in liver glycogen were monomeric, the glucose concentration in liver would be so high that cells would swell and lyse from the entry of water by osmosis.

Storage of Glucose as Polymers Avoids High Osmolarity

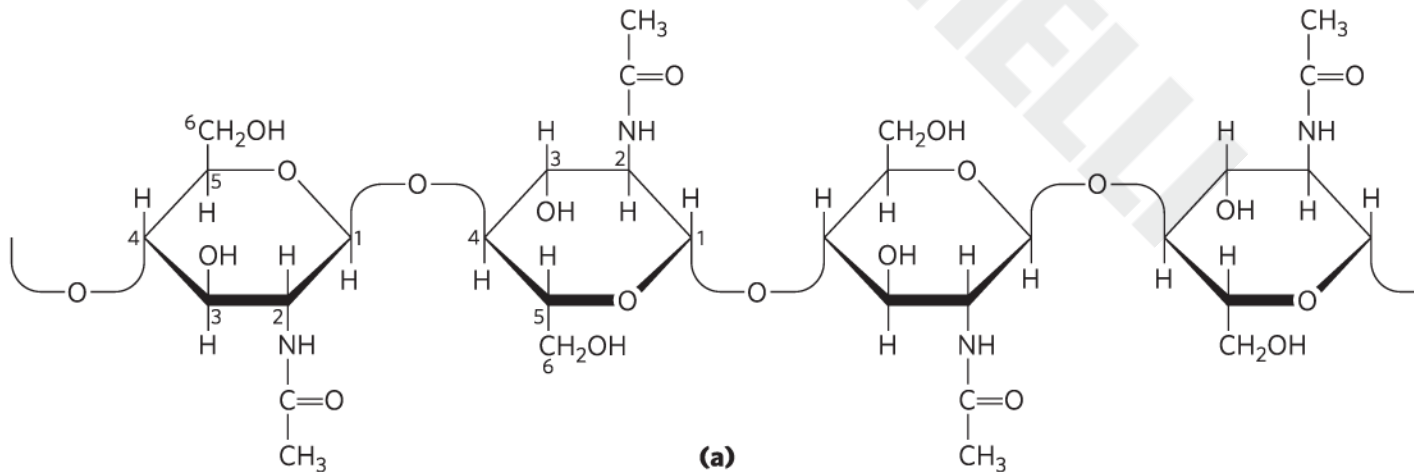
- hepatocytes in the fed state store glycogen equivalent to a glucose concentration of 0.4 M
- 0.4 M glucose in the cytosol would elevate the osmolarity
 - the resulting osmotic entry of water might rupture the cell

P5 Principle 5 (3 of 6)

Polysaccharides assume three-dimensional structures with the lowest-energy conformations, determined by covalent bonds, hydrogen bonds, charge interactions, and steric factors. Starch folds into a helical structure stabilized by internal hydrogen bonds; cellulose assumes an extended structure in which intermolecular hydrogen bonds are more important.

Chitin

- **chitin** = linear homopolysaccharide composed of *N*-acetylglucosamine residues in (β 1 \rightarrow 4) linkage
 - acetylated amino group makes chitin more hydrophobic and water-resistant than cellulose



(b)

(b) Paul Whitten/Science Source.

Principle 5 (4 of 6)

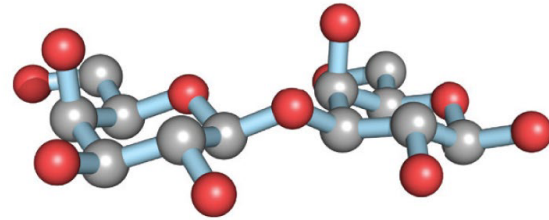
Polysaccharides assume three-dimensional structures with the lowest-energy conformations, determined by covalent bonds, hydrogen bonds, charge interactions, and steric factors. Starch folds into a helical structure stabilized by internal hydrogen bonds; cellulose assumes an extended structure in which intermolecular hydrogen bonds are more important.

Steric Factors and Hydrogen Bonding Influence Homopolysaccharide Folding

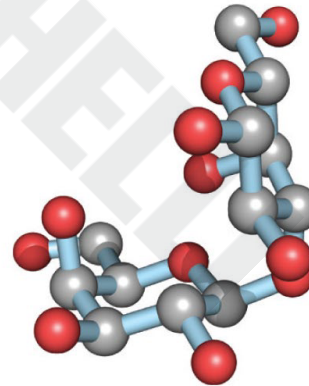
- three-dimensional structures stabilized by weak interactions within or between molecules
 - hydrogen bonding is especially important due to the high number of hydroxyl groups in polysaccharides
- free rotation about both C—O bonds linking the residues is limited by steric hindrance by substituents

Different Energetic Conformation of a Disaccharide

- bulkiness and electronic effects at the anomeric carbon place constraints on φ and ψ



Low-energy conformation is extended and maximizes H-bonding.



High-energy conformation is sterically hindered.

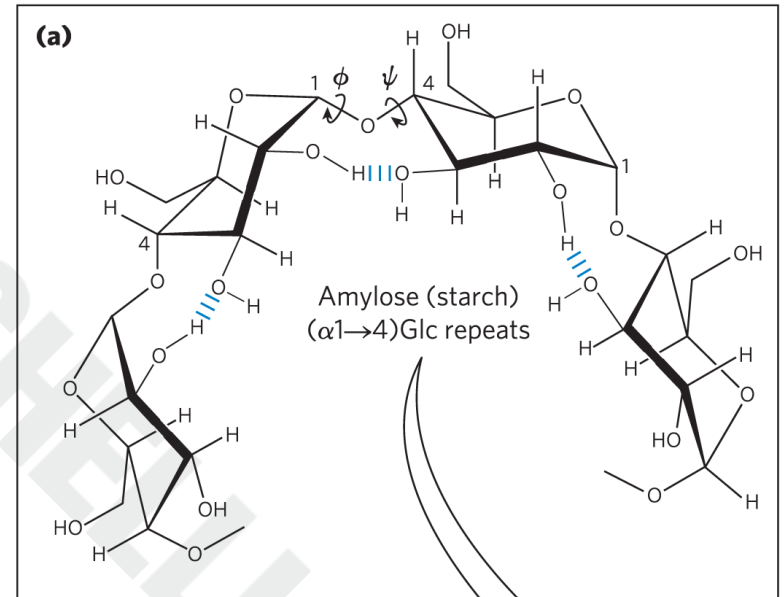
Nelson & Cox, *Lehninger Principles of Biochemistry*, 8e, © 2021 W. H. Freeman and Company

Principle 5 (5 of 6)

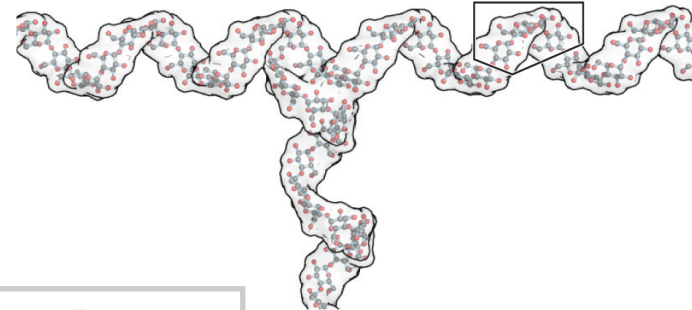
Polysaccharides assume three-dimensional structures with the lowest-energy conformations, determined by covalent bonds, hydrogen bonds, charge interactions, and steric factors. Starch folds into a helical structure stabilized by internal hydrogen bonds; cellulose assumes an extended structure in which intermolecular hydrogen bonds are more important.

Helical Structure of Starch and Glycogen

- most stable three-dimensional structure for the (α 1 \rightarrow 4)-linked chains of starch and glycogen
 - six residues/turn



(b)

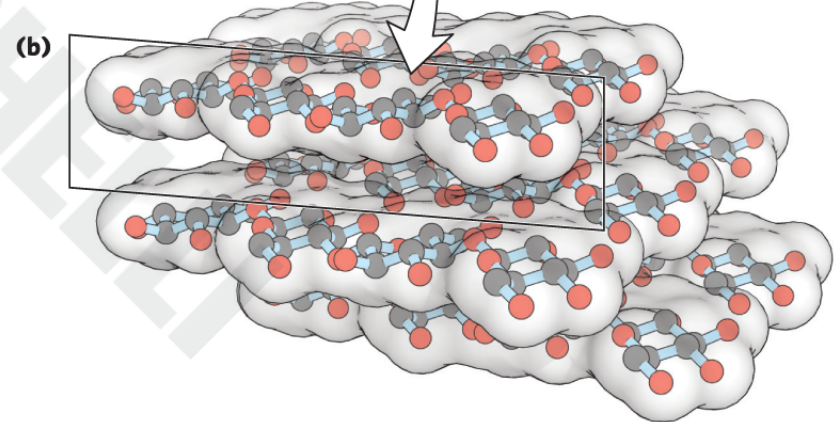
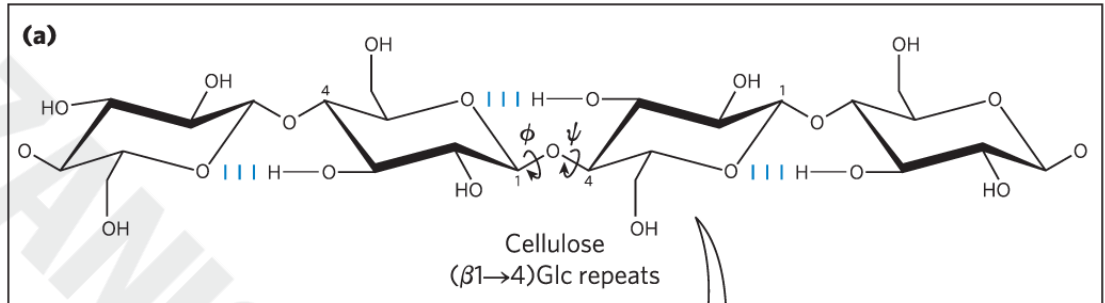


P5 Principle 5 (6 of 6)

Polysaccharides assume three-dimensional structures with the lowest-energy conformations, determined by covalent bonds, hydrogen bonds, charge interactions, and steric factors. Starch folds into a helical structure stabilized by internal hydrogen bonds; cellulose assumes an extended structure in which intermolecular hydrogen bonds are more important.

Linear Structure of Cellulose

- most stable conformation is a straight, extended chain
 - each chair is turned 180° relative to its neighbors



Principle 2 (3 of 3)

Monomeric subunits, monosaccharides, serve as the building blocks of large carbohydrate polymers. The specific sugar, the way the units are linked, and whether the polymer is branched determine its properties and thus its function.

Structure and Roles of Some Polysaccharides

Table 7-2 Structures and Roles of Some Polysaccharides

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

7.3 Glycoconjugates: Proteoglycans, Glycoproteins, and Glycolipids

Principle 6 (2 of 4)

Molecular complementarity is central to function.
The recognition of oligosaccharides by sugar-binding proteins (lectins) results from a perfect fit between lectin and ligand.

Glycoproteins

- **glycoproteins** = have one or several oligosaccharides joined covalently to a protein
 - found on the outer face of the plasma membrane, in ECM, in blood, and in organelles (Golgi complexes, secretory granules, and lysosomes)
 - oligosaccharide portions are heterogenous and rich in information

Glycolipids and Glycosphingolipids

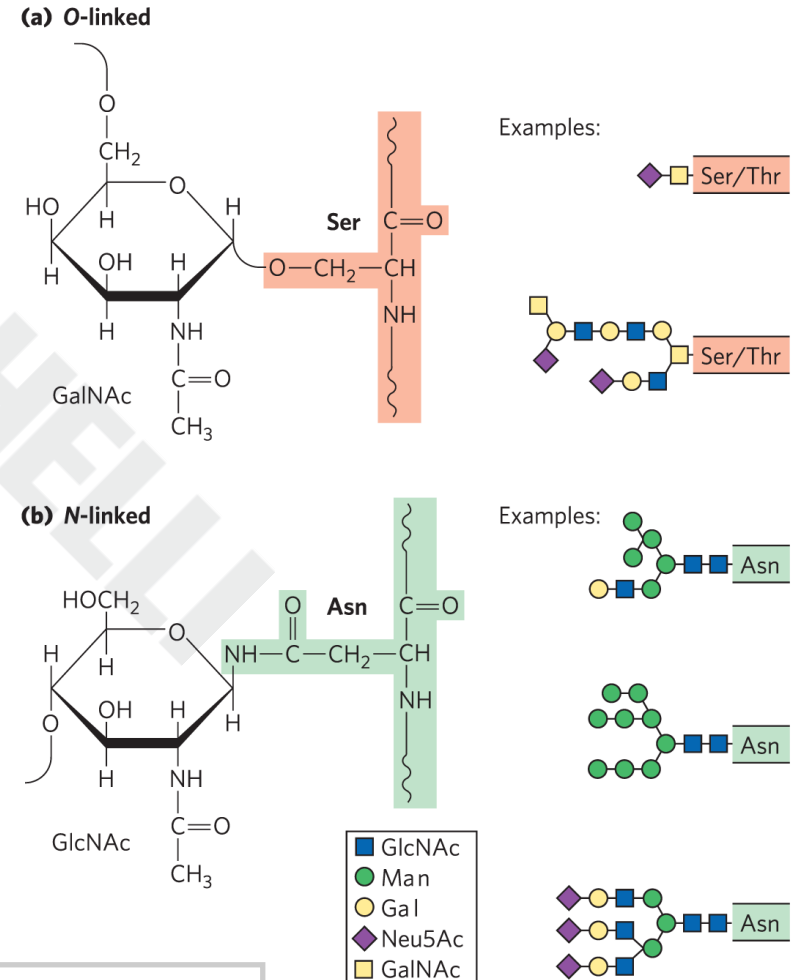
- **glycolipids** = plasma membrane components in which the hydrophilic head groups are oligosaccharides
- **glycosphingolipids** = class of glycolipids with specific backbone structure
 - neurons are rich in glycosphingolipids
 - play a role in signal transduction

Principle 7 (2 of 3)

An almost infinite variety of discrete structures can be built from a small number of monomeric subunits. Even short polymers, when arranged in different sequences, joined through different linkages, and branched to specific degrees, present unique faces recognized by their molecular partners.

Glycoproteins Have Covalently Attached Oligosaccharides

- two types of attachments:
 - O-linked = a glycoside bond joins the anomeric carbon of a carbohydrate to the —OH of a Ser or Thr residue
 - N-linked = an **N-glycosyl bond** joins the anomeric carbon of a sugar to the amide nitrogen of an Asn residue



Examples of Glycoproteins

- **mucins** = secreted or membrane glycoproteins
 - can contain large numbers of O-linked oligosaccharide chains
 - present in most secretions
- proteins of the blood
 - examples: immunoglobulins (antibodies), follicle-stimulating hormone, luteinizing hormone, and thyroid-stimulating hormone
- milk proteins
 - example: major whey protein α -lactalbumin

Principle 7 (3 of 3)

An almost infinite variety of discrete structures can be built from a small number of monomeric subunits. Even short polymers, when arranged in different sequences, joined through different linkages, and branched to specific degrees, present unique faces recognized by their molecular partners.

The Biological Advantages of Adding Oligosaccharides to Proteins

- covalently attached oligosaccharides:
 - influence the folding and stability of the proteins
 - provide critical information about the targeting of newly synthesized proteins
 - allow specific recognition by other proteins

Glycomics

- **glycomics** = the systematic characterization of all carbohydrate components of a given cell or tissue, including those attached to proteins and to lipids