# Macromolecules comparison table answer key

Inorganic compounds that do not contain both carbon and hydrogen. Start studying macromolecule comparison table eilers biology. Macromolecule Chart (Biomolecules) Table of contents what is the scientific method. Macromolecule comparison table worksheet. Acid only used once. Macromolecule monomer monomer diagram polymer function food sourcesexample nucleic acids nucleotide nucleic acid stores and transmits hereditary genetic. 121 short term energy storage structure cell walls exoskeletons monosaccharide glycogen chitin cellulose glucose fructose galactose sucrose lactose maltose. Classes of organic compounds that are central to life on earth. Macromolecule comparison chart organic macromolecules review chart with answers by warbler biology curricula macromolecule comparison table norr anatomy aset biology class carbohydrates and lipids table with drawers. Organic compounds that contain both carbon and hydrogen atoms. Vocabulary lessons getting nerdy science lessons. 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Organic Macromolecules Worksheet Macromolecules Chart Functions Examples Macro Pictures PPT - Macromolecules Graphic Organizer PowerPoint 1000+ images about Biology: Macromolecules on Pinterest Macromolecules Review Chart with Answers by Warbler What Elements Make Up Carbohydrates Lipids Proteins And Lee, Willie / Biology FA macromolecule foldable - Google Search | Interactive 10 Best Images of Macromolecules Graphic Organizer 4 types of macromolecules chart - Google Search Macromolecules Practice Bundle (Carbs, Lipids, Proteins Bio Macromolecule Worksheet - Macromolecules Practice Macromolecules Table Manipulative by Biology Made Easy | TpT Macromolecules in food lab | Biochemistry/Macromolecules Biomolecule Review Chart - Biomolecule Review Chart Lipids Macromolecules of Life Graphic Organizer by Science Macromolecules Chart Functions Examples Macro Pictures Biology Macromolecule Assessments with Chart by Bio4U High Organic Chemistry – Carbon Chemistry and Macromolecules Week 8 Macromolecules (Proteins,carbohydrates, lipids Macromolecules Review Chart for INB by Science Rocks | TpT If a monosaccharide has a carbonyl function on one of the inner atoms of the carbon chain it is classified as a ketose. Dihydroxyacetone may not be a sugar, but it is included as the ketose analog of glyceraldehyde. The carbonyl group is commonly found at C-2, as illustrated by the following examples (chiral centers are colored red). As expected, the carbonyl function of a ketose may be reduced by sodium borohydride, usually to a mixture of epimeric products. D-Fructose, the sweetest of the common natural sugars, is for example reduced to a mixture of D-glucitol (sorbitol) and D-mannitol, named after the aldohexoses from which they may also be obtained by analogous reduction. Mannitol is itself a common natural carbohydrate. Although the ketoses are distinct isomers of the aldose monosaccharides, the chemistry of both classes is linked due to their facile interconversion in the presence of acid or base catalysts. This interconversion, and the corresponding epimerization at sites alpha to the carbonyl functions, occurs by way of an enediol tautomeric intermediate. By clicking on the diagram, an equation illustrating these isomerizations will be displayed. Because of base-catalyzed isomerizations of this kind, the Tollens' reagent is not useful for distinguishing aldoses from ketoses or for specific oxidation of aldoses to the corresponding aldonic acids. Oxidation by HOBr is preferred for the latter conversion. Anomeric Forms of Glucose Fischer's brilliant elucidation of the configuration of glucose did not remove all uncertainty concerning its structure. Two different crystalline forms of glucose were reported in 1895. Each of these gave all the characteristic reactions of glucose, and when dissolved in water equilibrated to the same mixture. This equilibration takes place over a period of many minutes, and the change in optical activity that occurs is called mutarotation. These facts are summarized in the diagram below. When glucose was converted to its pentamethyl ether (reaction with excess CH3I & AgOH), two different isomers were isolated, and neither exhibited the expected aldehyde reactions. Acid-catalyzed hydrolysis of the pentamethyl ether derivatives, however, gave a tetramethyl derivative that was oxidized by Tollen's reagent and reduced by sodium borohydride, as expected for an aldehyde. These reactions will be displayed above by clicking on the diagram. The search for scientific truth often proceeds in stages, and the structural elucidation of glucose serves as a good example. It should be clear from the new evidence presented above, that the open chain pentahydroxyhexanal structure drawn above must be modified. Somehow a new stereogenic center must be created, and the aldehyde must be deactivated in the pentamethyl derivative. A simple solution to this dilemma is achieved by converting the open aldehyde structure for glucose into a cyclic hemiacetal, called a glucopyranose, as shown in the following diagram. The linear aldehyde is tipped on its side, and rotation about the C4-C5 bond brings the C5-hydroxyl function close to the aldehyde carbon. For ease of viewing, the six-membered hemiacetal structure is drawn as a flat hexagon, but it actually assumes a chair conformation. The hemiacetal carbon atom (C-1) becomes a new stereogenic center, commonly referred to as the anomeric carbon, and the α and β-isomers are called anomers. We can now consider how this modification of the glucose structure accounts for the puzzling facts noted above. First, we know that hemiacetals are in equilibrium with their carbonyl and alcohol components when in solution. Consequently, fresh solutions of either alpha or beta-glucose crystals in water should establish an equilibrium mixture of both anomers, plus the open chain chain form. This will be shown above by clicking on the diagram. Note that despite the very low concentration of the open chain aldehyde in this mixture, typical chemical reactions of aldehydes take place rapidly. Second, a pentamethyl ether derivative of the pyranose structure converts the hemiacetal function to an acetal. Acetals are stable to base, so this product should not react with Tollen's reagent or be reduced by sodium borohydride. Acid hydrolysis of acetals regenerates the carbonyl and alcohol components, and in the case of the glucose derivative this will be a tetramethyl ether of the pyranose hemiacetal. This compound will, of course, undergo typical aldehyde reactions. By clicking on the diagram a second time this relationship will be displayed above. 5. Cyclic Forms of Monosaccharides As noted above, the preferred structural form of many monosaccharides may be that of a cyclic hemiacetal. Five and six-membered rings are favored over other ring sizes because of their low angle and eclipsing strain. Cyclic structures of this kind are termed furanose (five-membered) or pyranose (six-membered), reflecting the ring size relationship to the common heterocyclic compounds furan and pyran shown on the right. Ribose, an important aldopentose, commonly adopts a furanose structure, as shown in the following illustration. By convention for the D-family, the five-membered furanose ring is drawn in an edgewise projection with the ring oxygen positioned away from the viewer. The anomeric carbon atom (colored red here) is placed on the right. The upper bond to this carbon is defined as beta, the lower bond then is alpha. Click on the following diagram to see a model of β-D-ribofuranose. The cyclic pyranose forms of various monosaccharides are often drawn in a flat projection known as a Haworth formula, after the British chemist, Norman Haworth. As with the furanose ring, the anomeric carbon is placed on the right with the ring oxygen to the back of the edgewise view. In the D-family, the alpha and beta bonds have the same orientation defined for the furanose ring (beta is up & alpha is down). These Haworth formulas are convenient for displaying stereochemical relationships, but do not represent the true shape of the molecules. We know that these molecules are actually puckered in a fashion we call a chair conformation. Examples of four typical pyranose structures are shown below, both as Haworth projections and as the more representative chair conformers. The anomeric carbons are colored red. Models of these glucose, galactose, mannose and allose pyranose structures may be viewed by Clicking Here. A practice page for examining the configurations of aldohexoses may be viewed by Clicking Here. The size of the cyclic hemiacetal ring adopted by a given sugar is not constant, but may vary with substituents and other structural features. Aldolhexoses usually form pyranose rings and their pentose homologs tend to prefer the furanose form, but there are many counter examples. The formation of acetal derivatives illustrates how subtle changes may alter this selectivity. By clicking on the above diagram. the display will change to illustrate this. A pyranose structure for D-glucose is drawn in the rose-shaded box on the left. Acetal derivatives have been prepared by acid-catalyzed reactions with benzaldehyde and acetone. As a rule, benzaldehyde forms six-membered cyclic acetals, whereas acetone prefers to form five-membered acetals. The top equation shows the formation and some reactions of the 4,6-O-benzylidene acetal, a commonly employed protective group. A methyl glycoside derivative of this compound (see below) leaves the C-2 and C-3 hydroxyl groups exposed to reactions such as the periodic acid cleavage, shown as the last step. The formation of an isopropylidene acetal at C-1 and C-2, center structure, leaves the C-3 hydroxyl as the only unprotected function. Selective oxidation to a ketone is then possible. Finally, direct di-O-isopropylidene derivatization of glucose by reaction with excess acetone results in a change to a furanose structure in which the C-3 hydroxyl is again unprotected. However, the same reaction with D-galactose, shown in the blue-shaded box, produces a pyranose product in which the C-6 hydroxyl is unprotected. Both derivatives do not react with Tollens' reagent. This difference in behavior is attributed to the cis-orientation of the C-3 and C-4 hydroxyl groups in galactose, which permits formation of a less strained five-membered cyclic acetal, compared with the trans-C-3 and C-4 hydroxyl groups in glucose. Derivatizations of this kind permit selective reactions to be conducted at different locations in these highly functionalized molecules. The ring size of these cyclic monosaccharides was determined by oxidation and chain cleavage of their tetra methyl ether derivatives. To see how this was done for glucose Click Here. 6. Glycosides Acetal derivatives formed when a monosaccharide reacts with an alcohol in the presence of an acid catalyst are called glycosides. This reaction is illustrated for glucose and methanol in the diagram below. In naming of glycosides, the "ose" suffix of the sugar name is replaced by "oside", and the alcohol group name is placed first. As is generally true for most acetals, glycoside formation involves the loss of an equivalent of water. The diether product is stable to base and alkaline oxidants such as Tollen's reagent. Since acid-catalyzed aldolization is reversible, glycosides may be hydrolyzed back to their alcohol and sugar components by aqueous acid. The anomeric methyl glucosides are formed in an equilibrium ratio of 66% alpha to 34% beta. From the structures in the previous diagram, we see that pyranose rings prefer chair conformations in which the largest number of substituents are equatorial. In the case of glucose, the substituents on the beta-anomer are all equatorial, whereas the C-1 substituent in the alpha-anomer changes to axial. Since substituents on cyclohexane rings prefer an equatorial location over axial (methoxycyclohexane is 75% equatorial), the preference for alpha-glycopyranoside formation is unexpected, and is referred to as the anomeric effect. Glycosides abound in biological systems. By attaching a sugar moiety to a lipid or benzenoid structure, the solubility and other properties of the compound may be changed substantially. Because of the important modifying influence of such derivatization, numerous enzyme systems, known as glycosidases, have evolved for the attachment and removal of sugars from alcohols, phenols and amines. Chemists refer to the sugar component of natural glycosides as the glycon and the alcohol component as the aglycon. Two examples of naturally occurring glycosides and one example of an amino derivative will be displayed above by clicking on the diagram. Salicin, one of the oldest herbal remedies known, was the model for the synthetic analgesic aspirin. A large class of hydroxylated, aromatic oxonium cations called anthocyanins provide the red, purple and blue colors of many flowers, fruits and some vegetables. Peonin is one example of this class of natural pigments, which exhibit a pronounced pH color dependence. The oxonium moiety is only stable in acidic environments, and the color changes or disappears when base is added. The complex changes that occur when wine is fermented and stored are in part associated with glycosides of anthocyanins. Finally, amino derivatives of ribose, such as cytidine play important roles in biological phosphorylating agents, coenzymes and information transport and storage materials. For a discussion of the anomeric effect Click Here. For examples of structurally and functionally modified sugars Click Here. Disaccharides When the alcohol component of a glycoside is provided by a hydroxyl function on another monosaccharide, the compound is called a disaccharide. Four examples of disaccharides composed of two glucose units are shown in the following diagram. The individual glucopyranose rings are labeled A and B, and the glycoside bonding is circled in light blue. Notice that the glycoside bond may be alpha, as in maltose and trehalose, or beta as in cellobiose and gentiobiose. Acid-catalyzed hydrolysis of these disaccharides yields glucose as the only product. Enzyme-catalyzed hydrolysis is selective for a specific glycoside bond, so an alpha-glycosidase cleaves maltose and trehalose to glucose, but does not cleave cellobiose or gentiobiose. A beta-glycosidase has the opposite activity. In order to draw a representative structure for cellobiose, one of the glucopyranose rings must be rotated by 180º, but this feature is often omitted in favor of retaining the usual perspective for the individual rings. The bonding between the glucopyranose rings in cellobiose and maltose is from the anomeric carbon in ring A to the C-4 hydroxyl group on ring B. This leaves the anomeric carbon in ring B free, so cellobiose and maltose both may assume alpha and beta anomers at that site (the beta form is shown in the diagram). Gentiobiose has a beta-glycoside link, originating at C-1 in ring A and terminating at C-6 in ring B. Its alpha-anomer is drawn in the diagram. Because cellobiose, maltose and gentiobiose are hemiacetals they are all reducing sugars (oxidized by Tollen's reagent). Trehalose, a disaccharide found in certain mushrooms, is a bis-acetal, and is therefore a non-reducing sugar. A systematic nomenclature for disaccharides exists, but as the following examples illustrate, these are often lengthy. Cellobiose : 4-O-β-D-Glucopyranosyl-D-glucose (the beta-anomer is drawn) Maltose : 4-O-α-D-Glucopyranosyl-D-glucose (the beta-anomer is drawn) Gentiobiose : 6-O-β-D-Glucopyranosyl-D-glucose (the alpha-anomer is drawn) Trehalose : α-D-Glucopyranosyl-α-D-glucopyranoside Although all the disaccharides shown here are made up of two glucopyranose rings, their properties differ in interesting ways. Maltose, sometimes called malt sugar, comes from the hydrolysis of starch. It is about one third as sweet as cane sugar (sucrose), is easily digested by humans, and is fermented by yeast. Cellobiose is obtained by the hydrolysis of cellulose. It has virtually no taste, is indigestible by humans, and is not fermented by yeast. Some bacteria have beta-glucosidase enzymes that hydrolyze the glycosidic bonds in cellobiose and cellulose. The presence of such bacteria in the digestive tracts of cows and termites permits these animals to use cellulose as a food. Finally, it may be noted that trehalose has a distinctly sweet taste, but gentiobiose is bitter. Disaccharides made up of other sugars are known, but glucose is often one of the components. Two important examples of such mixed disaccharides will be displayed above by clicking on the diagram. Lactose, also known as milk sugar, is a galactose-glucose compound joined as a beta-glycoside. It is a reducing sugar because of the hemiacetal function remaining in the glucose moiety. Many adults, particularly those from regions where milk is not a dietary staple, have a metabolic intolerance for lactose. Infants have a digestive enzyme which cleaves the beta-glycoside bond in lactose, but production of this enzyme stops with weaning. Cheese is less subject to the lactose intolerance problem, since most of the lactose is removed with the whey. Sucrose, or cane sugar, is our most commonly used sweetening agent. It is a non-reducing disaccharide composed of glucose and fructose joined at the anomeric carbon of each by glycoside bonds (one alpha and one beta). In the formula shown here the fructose ring has been rotated 180º from its conventional perspective. To examine a model of sucrose Click Here Additional Topics For a brief discussion of sweetening agents Click Here. For examples of some larger saccharide oligomers Click Here. Polysaccharides As the name implies, polysaccharides are large high-molecular weight molecules constructed by joining monosaccharide units together by glycosidic bonds. They are sometimes called glycans. The most important compounds in this class, cellulose, starch and glycogen are all polymers of glucose. This is easily demonstrated by acid-catalyzed hydrolysis to the monosaccharide. Since partial hydrolysis of cellulose gives varying amounts of cellobiose, we conclude the glucose units in this macromolecule are joined by beta-glycoside bonds between C-1 and C-4 sites of adjacent sugars. Partial hydrolysis of starch and glycogen produces the disaccharide maltose together with low molecular weight dextrans, polysaccharides in which glucose molecules are joined by alpha-glycoside links between C-1 and C-6, as well as the alpha C-1 to C-4 links found in maltose. Polysaccharides built from other monosaccharides (e.g. mannose, galactose, xylose and arabinose) are also known, but will not be discussed here. Over half of the total organic carbon in the earth's biosphere is in cellulose. Cotton fibers are essentially pure cellulose, and the wood of bushes and trees is about 50% cellulose. As a polymer of glucose, cellulose has the formula (C6H10O5)n where n ranges from 500 to 5,000, depending on the source of the polymer. The glucose units in cellulose are linked in a linear fashion, as shown in the drawing below. The beta-glycoside bonds permit these chains to stretch out, and this conformation is stabilized by intramolecular hydrogen bonds. A parallel orientation of adjacent chains is also favored by intermolecular hydrogen bonds. Although an individual hydrogen bond is relatively weak, many such bonds acting together can impart great stability to certain conformations of large molecules. Most animals cannot digest cellulose as a food, and in the diets of humans this part of our vegetable intake functions as roughage and is eliminated largely unchanged. Some animals (the cow and termites, for example) harbor intestinal microorganisms that breakdown cellulose into monosaccharide nutrients by the use of beta-glycosidase enzymes. Cellulose is commonly accompanied by a lower molecular weight, branched, amorphous polymer called hemicellulose. In contrast to cellulose, hemicellulose is structurally weak and is easily hydrolyzed by dilute acid or base. Also, many enzymes catalyze its hydrolysis. Hemicelluloses are composed of many D-pentose sugars, with xylose being the major component. Mannose and mannuronic acid are often present, as well as galactose and galacturonic acid. Starch is a polymer of glucose, found in roots, rhizomes, seeds, stems, tubers and corms of plants, as microscopic granules having characteristic shapes and sizes. Most animals, including humans, depend on these plant starches for nourishment. The structure of starch is more complex than that of cellulose. The intact granules are insoluble in cold water, but grinding or swelling them in warm water causes them to burst. The released starch consists of two fractions. About 20% is a water soluble material called amylose. Molecules of amylose are linear chains of several thousand glucose units joined by alpha C-1 to C-4 glycoside bonds. Amylose solutions are actually dispersions of hydrated helical micelles. The majority of the starch is a much higher molecular weight substance, consisting of nearly a million glucose units, and called amylopectin. Molecules of amylopectin are branched networks built from C-1 to C-4 and C-1 to C-6 glycoside links, and are essentially water insoluble. Representative structural formulas for amylose and amylopectin will be shown above by clicking on the diagram. To see an expanded structure for amylopectin click again on the diagram. The branching in this diagram is exaggerated, since on average, branches only occur every twenty five glucose units. Hydrolysis of starch, usually by enzymatic reactions, produces a syrupy liquid consisting largely of glucose. When cornstarch is the feedstock, this product is known as corn syrup. It is widely used to soften texture, add volume, prohibit crystallization and enhance the flavor of foods. Glycogen is the glucose storage polymer used by animals. It has a structure similar to amylopectin, but is even more highly branched (about every tenth glucose unit). The degree of branching in these polysaccharides may be measured by enzymatic or chemical analysis. For examples of chemical analysis of branching Click Here. Synthetic Modification of Cellulose Cotton, probably the most useful natural fiber, is nearly pure cellulose. The manufacture of textiles from cotton involves physical manipulation of the raw material by carding, combing and spinning selected fibers. For fabrics the best cotton has long fibers, and short fibers or cotton dust are removed. Crude cellulose is also available from wood pulp by dissolving the lignan matrix surrounding it. These less desirable cellulose sources are widely used for making paper. In order to expand the ways in which cellulose can be put to practical use, chemists have devised techniques for preparing solutions of cellulose derivatives that can be spun into fibers, spread into a film or cast in various solid forms. A key factor in these transformations are the three free hydroxyl groups on each glucose unit in the cellulose chain, –[C6H7O(OH)3]n–. Esterification of these functions leads to polymeric products having very different properties compared with cellulose itself. Cellulose Nitrate, first prepared over 150 years ago by treating cellulose with nitric acid, is the earliest synthetic polymer to see general use. The fully nitrated compound, –[C6H7O(ONO2)3]n–, called guncotton, is explosively flammable and is a component of smokeless powder. Partially nitrated cellulose is called pyroxylin. Pyroxylin is soluble in ether and at one time was used for photographic film and lacquers. The high flammability of pyroxylin caused many tragic cinema fires during its period of use. Furthermore, slow hydrolysis of pyroxylin yields nitric acid, a process that contributes to the deterioration of early motion picture films in storage. Cellulose Acetate, –[C6H7O(OAc)3]n–, is less flammable than pyroxylin, and has replaced it in most applications. It is prepared by reaction of cellulose with acetic anhydride and an acid catalyst. The properties of the product vary with the degree of acetylation. Some chain shortening occurs unavoidably in the preparations. An acetone solution of cellulose acetate may be forced through a spinneret to generate filaments, called acetate rayon, that can be woven into fabrics. Viscose Rayon, is prepared by formation of an alkali soluble xanthate derivative that can be spun into a fiber that reforms the cellulose polymer by acid quenching. The following general equation illustrates these transformations. The product fiber is called viscose rayon. ROH NaOH RO(-) Na(+) + S=C=S RO-CS2(-) Na(+) H3O(+) ROH cellulose viscose solution rayon Introduction Compare Glucose and Galactose Contributors Glyceraldehyde, the simplest carbohydrate, exhibits properties of a chiral or optical isomer compound. This molecule forms the basis for the designation of the isomers of all of the carbohydrates. Introduction Glyceraldehyde can exist in two isomeric forms that are mirror images of each other which are shown below. The absolute configuration is defined by the molecule on the far left as the D-glyceraldehyde. With the aldehyde group in the "up" direction, the the -OH group must project to the right side of the molecule for the D isomer. Chemists have used this configuration of D-glyceraldehyde to determine the optical isomer families of the rest of the carbohydrates. All naturally occurring monosaccharides belong to the D optical family. It is remarkable that the chemistry and enzymes of all living things can tell the difference between the geometry of one optical isomer over the other. Monosaccharides are assigned to the D-family according to the projection of the -OH group to the right on the chiral carbon that is the farthest from the carbonyl (aldehyde) group. This is on carbon # 5 if the carbonyl carbon is # 1. Note: For whatever reason, the ball and stick model does not completely match the projections of the -OH groups on carbons # 2 and 4. It is in the way that the flat Fischer model has been defined. How many chiral carbons can you find? List them. If necessary Review Chiral Compounds to find the definitions.Then check the answer from the drop down menu. Compare Glucose and Galactose Examine the structures of glucose and galactose carefully. Which -OH group determines that they both are the D isomer? Then check the answer from the drop down menu. Isomers have different arrangements of atoms. Which carbon bonding to -OH and -H is different in glucose vs. galactose? This single difference makes glucose and galactose isomers. Then check the answer from the drop down menu. Introduction Di- and Poly-Carbohydrates Metabolism Contributors Introduction The chemistry of carbohydrates most closely resembles that of alcohol, aldehyde, and ketone functional groups. As a result, the modern definition of a CARBOHYDRATE is that the compounds are polyhydroxy aldehydes or ketones. The chemistry of carbohydrates is complicated by the fact that there is a functional group (alcohol) on almost every carbon. In addition, the carbohydrate may exist in either a straight chain or a ring structure. Ring structures incorporate two additional functional groups: the hemiacetal and acetal. A major part of the carbon cycle occurs as carbon dioxide is converted to carbohydrates through photosynthesis. Carbohydrates are utilized by animals and humans in metabolism to produce energy and other compounds. Photosynthesis is a complex series of reactions carried out by algae, phytoplankton, and the leaves in plants, which utilize the energy from the sun. The simplified version of this chemical reaction is to utilize carbon dioxide molecules from the air and water molecules and the energy from the sun to produce a simple sugar such as glucose and oxygen molecules as a by product. The simple sugars are then converted into other molecules such as starch, fats, proteins, enzymes, and DNA/RNA i.e. all of the other molecules in living plants. All of the "matter/stuff" of a plant ultimately is produced as a result of this photosynthesis reaction. Di- and Poly-Carbohydrates Monosaccharides contain one sugar unit such as glucose, galactose, fructose, etc. Disaccharides contain two sugar units. In almost all cases one of the sugars is glucose, with the other sugar being galactose, fructose, or another glucose. Common disaccharides are maltose, lactose, and sucrose. Polysaccharides contain many sugar units in long polymer chains of many repeating units. The most common sugar unit is glucose. Common poly saccharides are starch, glycogen, and cellulose. Table 1: Common Carbohydrates Name Derivation of name and Source Monosaccharides Glucose From Greek word for sweet wine; grape sugar, blood sugar, dextrose. Galactose Greek word for milk–"galact", found as a component of lactose in milk. Fructose Latin word for fruit–"fructus", also known as levulose,found in fruits and honey; sweetest sugar. Ribose Ribose and Deoxyribose are found in the backbone structure of RNA and DNA, respectively. Disaccharides – contain two monosaccharides Sucrose French word for sugar–"sucre", a disaccharide containing glucose and fructose; table sugar, cane sugar, beet sugar. Lactose Latin word for milk–"lact"; a disaccharide found in milk containing glucose and galactose. Maltose French word for "malt"; a disaccharide containing two units of glucose; found in germinating grains, used to make beer. Common Polysaccharides Starch Plants store glucose as the polysaccharide starch. The cereal grains (wheat, rice, corn, oats, barley) as well as tubers such as potatoes are rich in starch. Cellulose The major component in the rigid cell walls in plants is cellulose and is a linear polysaccharide polymer with many glucose monosaccharide units. Glycogen This is the storage form of glucose in animals and humans which is analogous to the starch in plants. Glycogen is synthesized and stored mainly in the liver and the muscles. Metabolism Metabolism occurs in animals and humans after the ingestion of organic plant or animal foods. In the cells a series of complex reactions occurs with oxygen to convert for example glucose sugar into the products of carbon dioxide and water and ENERGY. This reaction is also carried out by bacteria in the decomposition/decay of waste materials on land and in the water. Combustion occurs when any organic material is reacted (burned) in the presence of oxygen to give off the products of carbon dioxide and water and ENERGY. The organic material can be any fossil fuel such as natural gas (methane), oil, or coal. Other organic materials that combust are wood, paper, plastics, and cloth. The whole purpose of both processes is to convert chemical energy into other forms of energy such as heat. Traditionally, in carbohydrate chemistry, the furanose rings and the pyranose rings in carbohydrate molecules are shown in the planar conformation, placed on the plane perpendicular to the plane of the paper.This representation of rings is known as the Haworth formula. eg: cyclic forms of D-glucoseTo generate the Haworth formulas of the cyclic forms of a monosaccharide, use the following procedure, explained using the pyranoses of D-glucose.Step 1: Draw the Fischer projection of the acyclic form of D-glucose. (See D,L convention)Step 2: Number the carbon chain in 1 starting at the top.Step 3: To generate the pyranose ring, the oxygen atom on C-5 in 1 needs to be attached to C-1 by a single bond.In 1, C-1 is behind the plane of the paper and the hydroxy group on C-5 is in front. For the pyranose ring to be planar, both C-1 and the hydroxy group on C-5 have to be either behind or in front of the plane of the paper. C-5 is a chiral center. In order to bring the hydroxy group on C-5 to the site occupied by the CH2OH group without changing the absolute configuration at C-5, rotate the three ligands H, OH, and CH2OH on C-5 in 1 clockwise without moving the fourth ligand. (See Fischer projection) 1 and 2 both represent D-glucose, but, in 2, unlike in 1, C-1 and the hydroxy group on C-5 are on the same side of the plane of the paper. Step 4: Ignore that 2 is a Fischer projection and rotate it clockwise by 90º. Step 5: Redraw the atom chain along the horizontal axis as follows. Step 6: Add the ligands on C-2 through C-5 in 4. The ligands pointing up in 3 are pointing up in 4; those pointing down in 3 are pointing down in 4. Step 7: Remove the hydrogen atom and the oxygen atom on C-1 and the hydrogen atom in the hydroxy group on C-5 in 5 and connect the two atoms by a single bond. Step 8: Add the two remaining bonds to C-1 in 6. Step 9: Attach a hydrogen atom to the bond pointing up and a hydroxy group to the bond pointing down on C-1 in 7. Step 10: Interchange the hydrogen atom and the hydroxy group on C-1 in 8. 8 and 9 are the Haworth formulas of the pyranoses of D-glucose. If, in the acyclic form of a monosaccharide, the hydroxy group that reacts with the carbonyl carbon is not on a chiral carbon (eg: D-fructose→pyranoses), skip step 3. LIPIDS Fatty acids are merely carboxylic acids with long hydrocarbon chains. The hydrocarbon chain length may vary from 10-30 carbons (most usual is 12-18). The non-polar hydrocarbon alkane chain is an important counter balance to the polar acid functional group. In acids with only a few carbons, the acid functional group dominates and gives the whole molecule a polar character. However, in fatty acids, the non-polar hydrocarbon chain gives the molecule a non-polar character. Fatty acids are merely carboxylic acids with long hydrocarbon chains. The hydrocarbon chain length may vary from 10-30 carbons (most usual is 12-18). The non-polar hydrocarbon alkane chain is an important counter balance to the polar acid functional group. In acids with only a few carbons, the acid functional group dominates and gives the whole molecule a polar character. However, in fatty acids, the non-polar hydrocarbon chain gives the molecule a non-polar character. Introduction The most common fatty acids are listed. Note that there are two groups of fatty acids–saturated and unsaturated. Recall that the term unsaturated refers to the presence of one or more double bonds between carbons as in alkenes. A saturated fatty acid has all bonding positions between carbons occupied by hydrogens. The melting points for the saturated fatty acids follow the boiling point principle observed previously. Melting point principle: as the molecular weight increases, the melting point increases. This observed in the series lauric (C12), palmitic (C16), stearic (C18). Room temperature is 25oC, Lauric acid which melts at 44o is still a solid, while arachidonic acid has long since melted at -50o, so it is a liquid at room temperature. Table 1: Common Fatty Acids Acid Name Structure Melting Point SATURATED Lauric CH3(CH2)10COOH +44 Palmitic CH3(CH2)14COOH +63 Stearic CH3(CH2)16COOH +70 UNSATURATED Oleic CH3(CH2)7CH=CH(CH2)7COOH +16 Linoleic CH3(CH2)4(CH=CHCH2)2(CH2)6COOH -5 Linolenic CH3CH2(CH=CHCH2)3(CH2)6COOH -11 Arachidonic CH3(CH2)4(CH=CHCH2)4(CH2)2COOH -50 Melting Points of Saturated vs. Unsaturated Fatty Acids Note that as a group, the unsaturated fatty acids have lower melting points than the saturated fatty acids. The reason for this phenomenon can be found by a careful consideration of molecular geometries. The tetrahedral bond angles on carbon results in a molecular geometry for saturated fatty acids that is relatively linear although with zigzags. See graphic on the left. This molecular structure allows many fatty acid molecules to be rather closely "stacked" together. As a result, close intermolecular interactions result in relatively high melting points. On the other hand, the introduction of one or more double bonds in the hydrocarbon chain in unsaturated fatty acids results in one or more "bends" in the molecule. The geometry of the double bond is almost always a cis configuration in natural fatty acids. and these molecules do not "stack" very well. The intermolecular interactions are much weaker than saturated molecules. As a result, the melting points are much lower for unsaturated fatty acids. Percent Fatty Acid Present in Triglycerides Fat or Oil Saturated Unsaturated Palmitic Stearic Oleic Linoleic Other Animal Origin Butter 29 9 27 4 31 Lard 30 18 41 6 5 Beef 32 25 38 3 2 Vegetable Origin Corn oil 10 4 34 48 4 Soybean 7 3 25 56 9 Peanut 7 5 60 21 7 Olive 6 4 83 7 – Hydrogenation Reaction Trans Fat References Contributors In the late 1970's the lipid hypothesis came in to existences stating that eating saturated fats leads to elevated LDL (Low Density Lipoprotein) which was perceived to be "bad cholesterol." This will result in coronary heart disease which is hardening and narrowing of arteries resulting in heart attack. Fats were eventually classified in to 2 categories: "healthy fats" and "unhealthy fats". Unhealthy fats where perceived to be saturated fats and healthy fats where perceived to be unsaturated fats.A meta-analysis of 72 studies with over 103,052 people have found no validity in the lipid hypothesis. The conclusion of the Meta-Analysis was,"In contrast to current recommendations, this systematic review found no evidence that saturated fat increases the risk of coronary disease, or that polyunsaturated fats have a cardio protective effect."[1] Dietary fats play a critical role in human health. They help keep cells healthy, help with brain development, help with the use of fat soluble vitamins, and they help cushion organs protecting them against blunt trauma. Fats come in multiple forms, saturated, unsaturated and trans fats just to name a few.Saturated fats are solid at room temperature due to their molecular shape. The term saturated is in reference to an sp3 carbon chain that has its remaining sp3 orbitals bonded with hydrogen atoms. Thus the term "saturated". It's "saturated" with hydrogen. Saturated fats have a chain like structure which allows them to stack very well forming a solid at room temperature. Unsaturated fats are not linear due to double bonded carbons which results in a different molecular shape because the sp2 carbons are trigonal planar, not tetrahedral (sp3 carbons) as the carbons are in saturated fats. This change in structure will cause the fat molecules to not stack very well resulting in fats that are liquid at room temperature. Butter is mostly saturated fat, that's why it's solid at room temperature. Olive Oil is liquid at room temperature, thus it's an unsaturated fat. An unsaturated fat can be made in to a saturated fat via hydrogenation reactions. Hydrogenation Reaction Unsaturated fatty acids may be converted to saturated fatty acids by the relatively simple hydrogenation reaction. Recall that the addition of hydrogen to an alkene (unsaturated) results in an alkane (saturated). A simple hydrogenation reaction is: H2C=CH2+H2→CH3CH3 alkene plus hydrogen yields an alkane Vegetable oils are commonly referred to as "polyunsaturated". This simply means that there are several double bonds present. Vegetable oils may be converted from liquids to solids by the hydrogenation reaction. Margarines and shortenings are "hardened" in this way to make them solid or semi-solids. Figure 1: Hydrogenation of a oleic fatty acid Vegetable oils which have been partially hydrogenated, are now partially saturated so the melting point increases to the point where a solid is present at room temperature. The degree of hydrogenation of unsaturated oils controls the final consistency of the product. What has happened to the healthfulness of the product which has been converted from unsaturated to saturated fats? Trans Fat A major health concern during the hydrogenation process is the production of trans fats. Trans fats are the result of a side reaction with the catalyst of the hydrogenation process. This is the result of an unsaturated fat which is normally found as a cis isomer converts to a trans isomer of the unsaturated fat. Isomers are molecules that have the same molecular formula but are bonded together differently. Focusing on the sp2 double bonded carbons, a cis isomer has the hydrogens on the same side. Due to the added energy from the hydrogenation process, the activation energy is reached to convert the cis isomers of the unsaturated fat to a trans isomer of the unsaturated fat. The effect is putting one of the hydrogens on the opposite side of one of the carbons. This results in a trans configuration of the double bonded carbons. The human body does not recognize trans fats. Although trans fatty acids are chemically "monounsaturated" or "polyunsaturated," they are considered so different from the cis monounsaturated or polyunsaturated fatty acids that they can not be legally designated as unsaturated for purposes of labeling. Most of the trans fatty acids (although chemically still unsaturated) produced by the partial hydrogenation process are now classified in the same category as saturated fats. The major negative is that trans fat tends to raise "bad" LDL- cholesterol and lower "good" HDL-cholesterol, although not as much as saturated fat. Trans fat are found in margarine, baked goods such as doughnuts and Danish pastry, deep-fried foods like fried chicken and French-fried potatoes, snack chips, imitation cheese, and confectionery fats. Prostaglandins were first discovered and isolated from human semen in the 1930s by Ulf von Euler of Sweden. Thinking they had come from the prostate gland, he named them prostaglandins. It has since been determined that they exist and are synthesized in virtually every cell of the body. Prostaglandins, are like hormones in that they act as chemical messengers, but do not move to other sites, but work right within the cells where they are synthesized. Introduction Prostaglandins are unsaturated carboxylic acids, consisting of of a 20 carbon skeleton that also contains a five member ring. They are biochemically synthesized from the fatty acid, arachidonic acid. See the graphic on the left. The unique shape of the arachidonic acid caused by a series of cis double bonds helps to put it into position to make the five member ring. See the prostaglandin in the next panel Prostaglandin Structure Prostaglandins are unsaturated carboxylic acids, consisting of of a 20 carbon skeleton that also contains a five member ring and are based upon the fatty acid, arachidonic acid. There are a variety of structures one, two, or three double bonds. On the five member ring there may also be double bonds, a ketone, or alcohol groups. A typical structure is on the left graphic. Functions of Prostaglandins There are a variety of physiological effects including: Activation of the inflammatory response, production of pain, and fever. When tissues are damaged, white blood cells flood to the site to try to minimize tissue destruction. Prostaglandins are produced as a result. Blood clots form when a blood vessel is damaged. A type of prostaglandin called thromboxane stimulates constriction and clotting of platelets. Conversely, PGI2, is produced to have the opposite effect on the walls of blood vessels where clots should not be forming. Certain prostaglandins are involved with the induction of labor and other reproductive processes. PGE2 causes uterine contractions and has been used to induce labor. Prostaglandins are involved in several other organs such as the gastrointestinal tract (inhibit acid synthesis and increase secretion of protective mucus), increase blood flow in kidneys, and leukotriens promote constriction of bronchi associated with asthma. Effects of Aspirin and other Pain Killers When you see that prostaglandins induce inflammation, pain, and fever, what comes to mind but aspirin. Aspirin blocks an enzyme called cyclooxygenase, COX-1 and COX-2, which is involved with the ring closure and addition of oxygen to arachidonic acid converting to prostaglandins. The acetyl group on aspirin is hydrolzed and then bonded to the alcohol group of serine as an ester. This has the effect of blocking the channel in the enzyme and arachidonic can not enter the active site of the enzyme. By inhibiting or blocking this enzyme, the synthesis of prostaglandins is blocked, which in turn relives some of the effects of pain and fever. Aspirin is also thought to inhibit the prostaglandin synthesis involved with unwanted blood clotting in coronary heart disease. At the same time an injury while taking aspirin may cause more extensive bleeding. Glycerides and waxes are lipids with have an ester as the major functional group and include: waxes, triglycerides, and phospholipids. Triglycerides are esters of fatty acids and a trifunctional alcohol – glycerol (IUPAC name is 1,2,3-propantriol). The properties of fats and oils follow the same general principles as already described for the fatty acids. The important properties to be considered are: melting points and degree of unsaturation from component fatty acids. Introduction Since glycerol has three alcohol functional groups, three fatty acids must react to make three ester functional groups. The three fatty acids may or may not be identical. In fact, three different fatty acids may be present. The synthesis of a triglyceride is another application of the ester synthesis reaction. To write the structure of the triglyceride you must know the structure of glycerol and be given or look up the structure of the fatty acid in the table. The common fats and oils including fatty acid content are listed below. Fat or Oil Saturated Unsaturated Palmitic Stearic Oleic Linoleic Other Animal Origin Butter 29 9 27 4 31 Lard 30 18 41 6 5 Beef 32 25 38 3 2 Vegetable Origin Corn oil 10 4 34 48 4 Soybean 7 3 25 56 9 Peanut 7 5 60 21 7 Olive 6 4 83 7 – Synthesis of a Triglyceride Since glycerol, (IUPAC name is 1,2,3-propantriol), has three alcohol functional groups, three fatty acids must react to make three ester functional groups. The three fatty acids may or may not be identical. In fact, three different fatty acids may be present. nThe synthesis of a triglyceride is another application of the ester synthesis reaction. To write the structure of the triglyceride you must know the structure of glycerol and be given or look up the structure of the fatty acid in the table – find lauric acid. Glycerol The simplified reaction reveals the process of breaking some bonds and forming the ester and the by product, water. Refer to the graphic on the left for the synthesis of trilauroylglycerol. First, the -OH (red) bond on the acid is broken and the -H (red) bond on the alcohol is also broken. Both join to make HOH, a water molecule. Secondly, the oxygen of the alcohol forms a bond (green) to the acid at the carbon with the double bond oxygen. This forms the ester functional group. This process is carried out three times to make three ester groups and three water molecules. Structure of a Triglyceride As you can see from the graphic on the left, the actual molecular model of the triglyceride does not look at all like the line drawing. The reason for this difference lies in the concepts of molecular geometry. Trilauroylglycerol. All of the above factors contribute to the apparent "T" shape of the molecule. Problems Quiz: Which acid (short chain or fatty) would most likely be soluble in water? 1 Practice writing out a triglyceride of stearic acid. Again look up the formula of stearic acid and use the structure of glycerol. 2. Write down your answers. Then check the answers from the drop down menu. What is the molecular geometry of all three carbons in glycerol (look at model above)? What is the molecular geometry of the carbon at the center of the ester group? What is the molecular geometry of the single bond oxygen? Introduction Lecithin Cephalins Contributors Phospholipids are similar to the triglycerides with a couple of exceptions. Phospholglycerides are esters of only two fatty acids, phosphoric acid and a trifunctional alcohol – glycerol (IUPAC name is 1,2,3-propantriol). The fatty acids are attached to the glycerol at the 1 and 2 positions on glycerol through ester bonds. There may be a variety of fatty acids, both saturated and unsatured, in the phospholipids. Introduction The third oxygen on glycerol is bonded to phosphoric acid through a phosphate ester bond (oxygen-phosphorus double bond oxygen). In addition, there is usually a complex amino alcohol also attached to the phosphate through a second phosphate ester bond. The complex amino alcohols include choline, ethanolamine, and the amino acid-serine. The properties of a phospholipid are characterized by the properties of the fatty acid chain and the phosphate/amino alcohol. The long hydrocarbon chains of the fatty acids are of course non-polar. The phosphate group has a negatively charged oxygen and a positively charged nitrogen to make this group ionic. In addition there are other oxygen of the ester groups, which make on whole end of the molecule strongly ionic and polar. Phospholipids are major components in the lipid bilayers of cell membranes. There are two common phospholipids: Lecithin contains the amino alcohol, choline. Cephalins contain the amino alcohols serine or ethanolamine Lecithin Lecithin is probably the most common phospholipid. It is found in egg yolks, wheat germ, and soybeans. Lecithin is extracted from soy beans for use as an emulsifying agent in foods. Lecithin is an emulsifier because it has both polar and non-polar properties, which enable it to cause the mixing of other fats and oils with water components. See more discussion on this property in soaps. Lecithin is also a major component in the lipid bilayers of cell membranes. Lecithin contains the ammonium salt of choline joined to the phosphate by an ester linkage. The nitrogen has a positive charge, just as in the ammonium ion. In choline, the nitrogen has the positive charge and has four methyl groups attached. Cephalins Cephalins are phosphoglycerides that contain ehtanolamine or the amino acid serine attached to the phosphate group through phosphate ester bonds. A variety of fatty acids make up the rest of the molecule. Cephalins are found in most cell membranes, particularly in brain tissues. They also iimportant in the blood clotting process as they are found in blood platelets. Note: The MEP coloration of the electrostatic potential does not show a strong red color for the phosphate-amino alcohol portion of the molecule as it should to show the strong polar property of that group. One major class of lipids is the steroids, which have structures totally different from the other classes of lipids. The main feature of steroids is the ring system of three cyclohexanes and one cyclopentane in a fused ring system as shown below. There are a variety of functional groups that may be attached. The main feature, as in all lipids, is the large number of carbon-hydrogens which make steroids non-polar. Introduction Steroids include such well known compounds as cholesterol, sex hormones, birth control pills, cortisone, and anabolic steroids. Cholesterol The best known and most abundant steroid in the body is cholesterol. Cholesterol is formed in brain tissue, nerve tissue, and the blood stream. It is the major compound found in gallstones and bile salts. Cholesterol also contributes to the formation of deposits on the inner walls of blood vessels. These deposits harden and obstruct the flow of blood. This condition, known as atherosclerosis, results in various heart diseases, strokes, and high blood pressure. Much research is currently underway to determine if a correlation exists between cholesterol levels in the blood and diet. Not only does cholesterol come from the diet, but cholesterol is synthesized in the body from carbohydrates and proteins as well as fat. Therefore, the elimination of cholesterol rich foods from the diet does not necessarily lower blood cholesterol levels. Some studies have found that if certain unsaturated fats and oils are substituted for saturated fats, the blood cholesterol level decreases. The research is incomplete on this problem. Structures of Sex Hormones Sex hormones are also steroids. The primary male hormone, testosterone, is responsible for the development of secondary sex characteristics. Two female sex hormones, progesterone and estrogen or estradiol control the ovulation cycle. Notice that the male and female hormones have only slight differences in structures, but yet have very different physiological effects. Testosterone promotes the normal development of male genital organs ans is synthesized from cholesterol in the testes. It also promotes secondary male sexual characteristics such as deep voice, facial and body hair. Estrogen, along with progesterone regulates changes occurring in the uterus and ovaries known as the menstrual cycle. For more details see Birth Control. Estrogen is synthesized from testosterone by making the first ring aromatic which results in mole double bonds, the loss of a methyl group and formation of an alcohol group. Adrenocorticoid Hormones The adrenocorticoid hormones are products of the adrenal glands ("adrenal" means adjacent to the renal (kidney). The most important mineralocrticoid is aldosterone, which regulates the reabsorption of sodium and chloride ions in the kidney tubules and increases the loss of potassium ions. Aldosterone is secreted when blood sodium ion levels are too low to cause the kidney to retain sodium ions. If sodium levels are elevated, aldosterone is not secreted, so that some sodium will be lost in the urine. Aldosterone also controls swelling in the tissues. Cortisol, the most important glucocortinoid, has the function of increasing glucose and glycogen concentrations in the body. These reactions are completed in the liver by taking fatty acids from lipid storage cells and amino acids from body proteins to make glucose and glycogen. In addition, cortisol and its ketone derivative, cortisone, have the ability to inflammatory effects. Cortisone or similar synthetic derivatives such as prednisolone are used to treat inflammatory diseases, rheumatoid arthritis, and bronchial asthma. There are many side effects with the use of cortisone drugs, so there use must be monitored carefully. The large molecules necessary for life that are built from smaller organic molecules are called biological macromolecules. There are four major classes of biological macromolecules (carbohydrates, lipids, proteins, and nucleic acids), and each is an important component of the cell and performs a wide array of functions. Combined, these molecules make up the majority of a cell's mass. Biological macromolecules are organic, meaning that they contain carbon. In addition, they may contain hydrogen, oxygen, nitrogen, phosphorus, sulfur, and additional minor elements. It is often said that life is "carbon-based." This means that carbon atoms, bonded to other carbon atoms or other elements, form the fundamental components of many, if not most, of the molecules found uniquely in living things. Other elements play important roles in biological molecules, but carbon certainly qualifies as the "foundation" element for molecules in living things. It is the bonding properties of carbon atoms that are responsible for its important role. Carbon contains four electrons in its outer shell. Therefore, it can form four covalent bonds with other atoms or molecules. The simplest organic carbon molecule is methane (CH4), in which four hydrogen atoms bind to a carbon atom. Figure 2.12 Carbon can form four covalent bonds to create an organic molecule. The simplest carbon molecule is methane (CH4), depicted here. However, structures that are more complex are made using carbon. Any of the hydrogen atoms can be replaced with another carbon atom covalently bonded to the first carbon atom. In this way, long and branching chains of carbon compounds can be made (Figure 2.13 a). The carbon atoms may bond with atoms of other elements, such as nitrogen, oxygen, and phosphorus (Figure 2.13 b). The molecules may also form rings, which themselves can link with other rings (Figure 2.13 c). This diversity of molecular forms accounts for the diversity of functions of the biological macromolecules and is based to a large degree on the ability of carbon to form multiple bonds with itself and other atoms. Figure 2.13 These examples show three molecules (found in living organisms) that contain carbon atoms bonded in various ways to other carbon atoms and the atoms of other elements. (a) This molecule of stearic acid has a long chain of carbon atoms. (b) Glycine, a component of proteins, contains carbon, nitrogen, oxygen, and hydrogen atoms. (c) Glucose, a sugar, has a ring of carbon atoms and one oxygen atom. Carbohydrates are macromolecules with which most consumers are somewhat familiar. To lose weight, some individuals adhere to "low-carb" diets. Athletes, in contrast, often "carb-load" before important competitions to ensure that they have sufficient energy to compete at a high level. Carbohydrates are, in fact, an essential part of our diet; grains, fruits, and vegetables are all natural sources of carbohydrates. Carbohydrates provide energy to the body, particularly through glucose, a simple sugar. Carbohydrates also have other important functions in humans, animals, and plants. Carbohydrates can be represented by the formula (CH2O)n, where n is the number of carbon atoms in the molecule. In other words, the ratio of carbon to hydrogen to oxygen is 1:2:1 in carbohydrate molecules. Carbohydrates are classified into three subtypes: monosaccharides, disaccharides, and polysaccharides. Monosaccharides (mono- = "one"; sacchar- = "sweet") are simple sugars, the most common of which is glucose. In monosaccharides, the number of carbon atoms usually ranges from three to six. Most monosaccharide names end with the suffix -ose. Depending on the number of carbon atoms in the sugar, they may be known as trioses (three carbon atoms), pentoses (five carbon atoms), and hexoses (six carbon atoms). Monosaccharides may exist as a linear chain or as ring-shaped molecules; in aqueous solutions, they are usually found in the ring form. The chemical formula for glucose is C6H12O6. In most living species, glucose is an important source of energy. During cellular respiration, energy is released from glucose, and that energy is used to help make adenosine triphosphate (ATP). Plants synthesize glucose using carbon dioxide and water by the process of photosynthesis, and the glucose, in turn, is used for the energy requirements of the plant. The excess synthesized glucose is often stored as starch that is broken down by other organisms that feed on plants. Galactose (part of lactose, or milk sugar) and fructose (found in fruit) are other common monosaccharides. Although glucose, galactose, and fructose all have the same chemical formula (C6H12O6), they differ structurally and chemically (and are known as isomers) because of differing arrangements of atoms in the carbon chain. Figure 2.14 Glucose, galactose, and fructose are isomeric monosaccharides, meaning that they have the same chemical formula but slightly different structures. Disaccharides (di- = "two") form when two monosaccharides undergo a dehydration reaction (a reaction in which the removal of a water molecule occurs). During this process, the hydroxyl group (–OH) of one monosaccharide combines with a hydrogen atom of another monosaccharide, releasing a molecule of water (H2O) and forming a covalent bond between atoms in the two sugar molecules. Common disaccharides include lactose, maltose, and sucrose. Lactose is a disaccharide consisting of the monomers glucose and galactose. It is found naturally in milk. Maltose, or malt sugar, is a disaccharide formed from a dehydration reaction between two glucose molecules. The most common disaccharide is sucrose, or table sugar, which is composed of the monomers glucose and fructose. A long chain of monosaccharides linked by covalent bonds is known as a polysaccharide (poly- = "many"). The chain may be branched or unbranched, and it may contain different types of monosaccharides. Polysaccharides may be very large molecules. Starch, glycogen, cellulose, and chitin are examples of polysaccharides. Starch is the stored form of sugars in plants and is made up of amylose and amylopectin (both polymers of glucose). Plants are able to synthesize glucose, and the excess glucose is stored as starch in different plant parts, including roots and seeds. The starch that is consumed by animals is broken down into smaller molecules, such as glucose. The cells can then absorb the glucose. Glycogen is the storage form of glucose in humans and other vertebrates, and is made up of monomers of glucose. Glycogen is the animal equivalent of starch and is a highly branched molecule usually stored in liver and muscle cells. Whenever glucose levels decrease, glycogen is broken down to release glucose. Cellulose is one of the most abundant natural biopolymers. The cell walls of plants are mostly made of cellulose, which provides structural support to the cell. Wood and paper are mostly cellulosic in nature. Cellulose is made up of glucose monomers that are linked by bonds between particular carbon atoms in the glucose molecule. Every other glucose monomer in cellulose is flipped over and packed tightly as extended long chains. This gives cellulose its rigidity and high tensile strength—which is so important to plant cells. Cellulose passing through our digestive system is called dietary fiber. While the glucose-glucose bonds in cellulose cannot be broken down by human digestive enzymes, herbivores such as cows, buffalos, and horses are able to digest grass that is rich in cellulose and use it as a food source. In these animals, certain species of bacteria reside in the rumen (part of the digestive system of herbivores) and secrete the enzyme cellulase. The appendix also contains bacteria that break down cellulose, giving it an important role in the digestive systems of ruminants. Cellulases can break down cellulose into glucose monomers that can be used as an energy source by the animal. Carbohydrates serve other functions in different animals. Arthropods, such as insects, spiders, and crabs, have an outer skeleton, called the exoskeleton, which protects their internal body parts. This exoskeleton is made of the biological macromolecule chitin, which is a nitrogenous carbohydrate. It is made of repeating units of a modified sugar containing nitrogen. Thus, through differences in molecular structure, carbohydrates are able to serve the very different functions of energy storage (starch and glycogen) and structural support and protection (cellulose and chitin). Figure 2.15 Although their structures and functions differ, all polysaccharide carbohydrates are made up of monosaccharides and have the chemical formula (CH2O)n. Registered Dietitian: Obesity is a worldwide health concern, and many diseases, such as diabetes and heart disease, are becoming more prevalent because of obesity. This is one of the reasons why registered dietitians are increasingly sought after for advice. Registered dietitians help plan food and nutrition programs for individuals in various settings. They often work with patients in health-care facilities, designing nutrition plans to prevent and treat diseases. For example, dietitians may teach a patient with diabetes how to manage blood-sugar levels by eating the correct types and amounts of carbohydrates. Dietitians may also work in nursing homes, schools, and private practices. To become a registered dietitian, one needs to earn at least a bachelor's degree in dietetics, nutrition, food technology, or a related field. In addition, registered dietitians must complete a supervised internship program and pass a national exam. Those who pursue careers in dietetics take courses in nutrition, chemistry, biochemistry, biology, microbiology, and human physiology. Dietitians must become experts in the chemistry and functions of food (proteins, carbohydrates, and fats). Lipids include a diverse group of compounds that are united by a common feature. Lipids are hydrophobic (“water-fearing”), or insoluble in water, because they are nonpolar molecules. This is because they are hydrocarbons that include only nonpolar carbon-carbon or carbon-hydrogen bonds. Lipids perform many different functions in a cell. Cells store energy for long-term use in the form of lipids called fats. Lipids also provide insulation from the environment for plants and animals. For example, they help keep aquatic birds and mammals dry because of their water-repelling nature. Lipids are also the building blocks of many hormones and are an important constituent of the plasma membrane. Lipids include fats, oils, waxes, phospholipids, and steroids. Figure 2.16 Hydrophobic lipids in the fur of aquatic mammals, such as this river otter, protect them from the elements. (credit: Ken Bosma) A fat molecule, such as a triglyceride, consists of two main components—glycerol and fatty acids. Glycerol is an organic compound with three carbon atoms, five hydrogen atoms, and three hydroxyl (–OH) groups. Fatty acids have a long chain of hydrocarbons to which an acidic carboxyl group is attached, hence the name “fatty acid.” The number of carbons in the fatty acid may range from 4 to 36; most common are those containing 12–18 carbons. In a fat molecule, a fatty acid is attached to each of the three oxygen atoms in the –OH groups of the glycerol molecule with a covalent bond. Figure 2.17 Lipids include fats, such as triglycerides, which are made up of fatty acids and glycerol, phospholipids, and steroids. During this covalent bond formation, three water molecules are released. The three fatty acids in the fat may be similar or dissimilar. These fats are also called triglycerides because they have three fatty acids. Some fatty acids have common names that specify their origin. For example, palmitic acid, a saturated fatty acid, is derived from the palm tree. Arachidic acid is derived from Arachis hypogaea, the scientific name for peanuts. Fatty acids may be saturated or unsaturated. In a fatty acid chain, if there are only single bonds between neighboring carbons in the hydrocarbon chain, the fatty acid is saturated. Saturated fatty acids are saturated with hydrogen; in other words, the number of hydrogen atoms attached to the carbon skeleton is maximized. When the hydrocarbon chain contains a double bond, the fatty acid is an unsaturated fatty acid. Most unsaturated fats are liquid at room temperature and are called oils. If there is one double bond in the molecule, then it is known as a monounsaturated fat (e.g., olive oil), and if there is more than one double bond, then it is known as a polyunsaturated fat (e.g., canola oil). Saturated fats tend to get packed tightly and are solid at room temperature. Animal fats with stearic acid and palmitic acid contained in meat, and the fat with butyric acid contained in butter, are examples of saturated fats. Mammals store fats in specialized cells called adipocytes, where globules of fat occupy most of the cell. In plants, fat or oil is stored in seeds and is used as a source of energy during embryonic development. Unsaturated fats or oils are usually of plant origin and contain unsaturated fatty acids. The double bond causes a bend or a “kink” that prevents the fatty acids from packing tightly, keeping them liquid at room temperature. Olive oil, corn oil, canola oil, and cod liver oil are examples of unsaturated fats. Unsaturated fats help to improve blood cholesterol levels, whereas saturated fats contribute to plaque formation in the arteries, which increases the risk of a heart attack. In the food industry, oils are artificially hydrogenated to make them semi-solid, leading to less spoilage and increased shelf life. Simply speaking, hydrogen gas is bubbled through oils to solidify them. During this hydrogenation process, double bonds of the cis-conformation in the hydrocarbon chain may be converted to double bonds in the trans-conformation. This forms a trans-fat from a cis-fat. The orientation of the double bonds affects the chemical properties of the fat. Figure 2.18 During the hydrogenation process, the orientation around the double bonds is changed, making a trans-fat from a cis-fat. This changes the chemical properties of the molecule. Margarine, some types of peanut butter, and shortening are examples of artificially hydrogenated trans-fats. Recent studies have shown that an increase in trans-fats in the human diet may lead to an increase in levels of low-density lipoprotein (LDL), or “bad” cholesterol, which, in turn, may lead to plaque deposition in the arteries, resulting in heart disease. Many fast food restaurants have recently eliminated the use of trans-fats, and U.S. food labels are now required to list their trans-fat content. Essential fatty acids are fatty acids that are required but not synthesized by the human body. Consequently, they must be supplemented through the diet. Omega-3 fatty acids fall into this category and are one of only two known essential fatty acids for humans (the other being omega-6 fatty acids). They are a type of polyunsaturated fat and are called omega-3 fatty acids because the third carbon from the end of the fatty acid participates in a double bond. Salmon, trout, and tuna are good sources of omega-3 fatty acids. Omega-3 fatty acids are important in brain function and normal growth and development. They may also prevent heart disease and reduce the risk of cancer. Like carbohydrates, fats have received a lot of bad publicity. It is true that eating an excess of fried foods and other “fatty” foods leads to weight gain. However, fats do have important functions. Fats serve as long-term energy storage. They also provide insulation for the body. Therefore, “healthy” unsaturated fats in moderate amounts should be consumed on a regular basis. Phospholipids are the major constituent of the plasma membrane. Like fats, they are composed of fatty acid chains attached to a glycerol or similar backbone. Instead of three fatty acids attached, however, there are two fatty acids and the third carbon of the glycerol backbone is bound to a phosphate group. The phosphate group is modified by the addition of an alcohol. A phospholipid has both hydrophobic and hydrophilic regions. The fatty acid chains are hydrophobic and exclude themselves from water, whereas the phosphate is hydrophilic and interacts with water. Cells are surrounded by a membrane, which has a bilayer of phospholipids. The fatty acids of phospholipids face inside, away from water, whereas the phosphate group can face either the outside environment or the inside of the cell, which are both aqueous. Unlike the phospholipids and fats discussed earlier, steroids have a ring structure. Although they do not resemble other lipids, they are grouped with them because they are also hydrophobic. All steroids have four, linked carbon rings and several of them, like cholesterol, have a short tail. Cholesterol is a steroid. Cholesterol is mainly synthesized in the liver and is the precursor of many steroid hormones, such as testosterone and estradiol. It is also the precursor of vitamins E and K. Cholesterol is the precursor of bile salts, which help in the breakdown of fats and their subsequent absorption by cells. Although cholesterol is often spoken of in negative terms, it is necessary for the proper functioning of the body. It is a key component of the plasma membranes of animal cells. Waxes are made up of a hydrocarbon chain with an alcohol (–OH) group and a fatty acid. Examples of animal waxes include beeswax and lanolin. Plants also have waxes, such as the coating on their leaves, that helps prevent them from drying out. For an additional perspective on lipids, explore “Biomolecules: The Lipids” through this interactive animation. Proteins are one of the most abundant organic molecules in living systems and have the most diverse range of functions of all macromolecules. Proteins may be structural, regulatory, contractile, or protective; they may serve in transport, storage, or membranes; or they may be toxins or enzymes. Each cell in a living system may contain thousands of different proteins, each with a unique function. Their structures, like their functions, vary greatly. They are all, however, polymers of amino acids, arranged in a linear sequence. The functions of proteins are very diverse because there are 20 different chemically distinct amino acids that form long chains, and the amino acids can be in any order. For example, proteins can function as enzymes or hormones. Enzymes, which are produced by living cells, are catalysts in biochemical reactions (like digestion) and are usually proteins. Each enzyme is specific for the substrate (a reactant that binds to an enzyme) upon which it acts. Enzymes can function to break molecular bonds, to rearrange bonds, or to form new bonds. An example of an enzyme is salivary amylase, which breaks down amylose, a component of starch. Hormones are chemical signaling molecules, usually proteins or steroids, secreted by an endocrine gland or group of endocrine cells that act to control or regulate specific physiological processes, including growth, development, metabolism, and reproduction. For example, insulin is a protein hormone that maintains blood glucose levels. Proteins have different shapes and molecular weights; some proteins are globular in shape whereas others are fibrous in nature. For example, hemoglobin is a globular protein, but collagen, found in our skin, is a fibrous protein. Protein shape is critical to its function. Changes in temperature, pH, and exposure to chemicals may lead to permanent changes in the shape of the protein, leading to a loss of function or denaturation (to be discussed in more detail later). All proteins are made up of different arrangements of the same 20 kinds of amino acids. Amino acids are the monomers that make up proteins. Each amino acid has the same fundamental structure, which consists of a central carbon atom bonded to an amino group (–$NH_2$), a carboxyl group (–COOH), and a hydrogen atom. Every amino acid also has another variable atom or group of atoms bonded to the central carbon atom known as the R group. The R group is the only difference in structure between the 20 amino acids; otherwise, the amino acids are identical. Figure 2.19 Amino acids are made up of a central carbon bonded to an amino group (–$NH_2$), a carboxyl group (–COOH), and a hydrogen atom. The central carbon’s fourth bond varies among the different amino acids, as seen in these examples of alanine, valine, lysine, and aspartic acid. The chemical nature of the R group determines the chemical nature of the amino acid within its protein (that is, whether it is acidic, basic, polar, or nonpolar). The sequence and number of amino acids ultimately determine a protein’s shape, size, and function. Each amino acid is attached to another amino acid by a covalent bond, known as a peptide bond, which is formed by a dehydration reaction. The carboxyl group of one amino acid and the amino group of a second amino acid combine, releasing a water molecule. The resulting bond is the peptide bond. The products formed by such a linkage are called polypeptides. While the terms polypeptide and protein are sometimes used interchangeably, a polypeptide is technically a polymer of amino acids, whereas the term protein is used for a polypeptide or polypeptides that have combined together, have a distinct shape, and have a unique function. The Evolutionary Significance of Cytochrome cCytochrome c is an important component of the molecular machinery that harvests energy from glucose. Because this protein’s role in producing cellular energy is crucial, it has changed very little over millions of years. Protein sequencing has shown that there is a considerable amount of sequence similarity among cytochrome c molecules of different species; evolutionary relationships can be assessed by measuring the similarities or differences among various species’ protein sequences. For example, scientists have determined that human cytochrome c contains 104 amino acids. For each cytochrome c molecule that has been sequenced to date from different organisms, 37 of these amino acids appear in the same position in each cytochrome c. This indicates that all of these organisms are descended from a common ancestor. On comparing the human and chimpanzee protein sequences, no sequence difference was found. When human and rhesus monkey sequences were compared, a single difference was found in one amino acid. In contrast, human-to-yeast comparisons show a difference in 44 amino acids, suggesting that humans and chimpanzees have a more recent common ancestor than humans and the rhesus monkey, or humans and yeast. As discussed earlier, the shape of a protein is critical to its function. To understand how the protein gets its final shape or conformation, we need to understand the four levels of protein structure: primary, secondary, tertiary, and quaternary. The unique sequence and number of amino acids in a polypeptide chain is its primary structure. The unique sequence for every protein is ultimately determined by the gene that encodes the protein. Any change in the gene sequence may lead to a different amino acid being added to the polypeptide chain, causing a change in protein structure and function. In sickle cell anemia, the hemoglobin β chain has a single amino acid substitution, causing a change in both the structure and function of the protein. What is most remarkable to consider is that a hemoglobin molecule is made up of two alpha chains and two beta chains that each consist of about 150 amino acids. The molecule, therefore, has about 600 amino acids. The structural difference between a normal hemoglobin molecule and a sickle cell molecule—that dramatically decreases life expectancy in the affected individuals—is a single amino acid of the 600. Because of this change of one amino acid in the chain, the normally biconcave, or disc-shaped, red blood cells assume a crescent or “sickle” shape, which clogs arteries. This can lead to a myriad of serious health problems, such as breathlessness, dizziness, headaches, and abdominal pain for those who have this disease. Folding patterns resulting from interactions between the non-R group portions of amino acids give rise to the secondary structure of the protein. The most common are the alpha (α)-helix and beta (β)-pleated sheet structures. Both structures are held in shape by hydrogen bonds. In the alpha helix, the bonds form between every fourth amino acid and cause a twist in the amino acid chain. In the β-pleated sheet, the “pleats” are formed by hydrogen bonding between atoms on the backbone of the polypeptide chain. The R groups are attached to the carbons, and extend above and below the folds of the pleat. The pleated segments align parallel to each other, and hydrogen bonds form between the same pairs of atoms on each of the aligned amino acids. The α-helix and β-pleated sheet structures are found in many globular and fibrous proteins. The unique three-dimensional structure of a polypeptide is known as its tertiary structure. This structure is caused by chemical interactions between various amino acids and regions of the polypeptide. Primarily, the interactions among R groups create the complex three-dimensional tertiary structure of a protein. There may be ionic bonds formed between R groups on different amino acids, or hydrogen bonding beyond that involved in the secondary structure. When protein folding takes place, the hydrophobic R groups of nonpolar amino acids lay in the interior of the protein, whereas the hydrophilic R groups lay on the outside. The former types of interactions are also known as hydrophobic interactions. In nature, some proteins are formed from several polypeptides, also known as subunits, and the interaction of these subunits forms the quaternary structure. Weak interactions between the subunits help to stabilize the overall structure. For example, hemoglobin is a combination of four polypeptide subunits. Figure 2.20 The four levels of protein structure can be observed in these illustrations. (credit: modification of work by National Human Genome Research Institute) Each protein has its own unique sequence and shape held together by chemical interactions. If the protein is subject to changes in temperature, pH, or exposure to chemicals, the protein structure may change, losing its shape in what is known as denaturation as discussed earlier. Denaturation is often reversible because the primary structure is preserved if the denaturing agent is removed, allowing the protein to resume its function. Sometimes denaturation is irreversible, leading to a loss of function. One example of protein denaturation can be seen when an egg is fried or boiled. The albumin protein in the liquid egg white is denatured when placed in a hot pan, changing from a clear substance to an opaque white substance. Not all proteins are denatured at high temperatures; for instance, bacteria that survive in hot springs have proteins that are adapted to function at those temperatures. For an additional perspective on proteins, explore “Biomolecules: The Proteins” through this interactive animation. Nucleic acids are key macromolecules in the continuity of life. They carry the genetic blueprint of a cell and carry instructions for the functioning of the cell. The two main types of nucleic acids are deoxyribonucleic acid (DNA) and ribonucleic acid (RNA). DNA is the genetic material found in all living organisms, ranging from single-celled bacteria to multicellular mammals. The other type of nucleic acid, RNA, is mostly involved in protein synthesis. The DNA molecules never leave the nucleus, but instead use an RNA intermediary to communicate with the rest of the cell. Other types of RNA are also involved in protein synthesis and its regulation. DNA and RNA are made up of monomers known as nucleotides. The nucleotides combine with each other to form a polynucleotide, DNA or RNA. Each nucleotide is made up of three components: a nitrogenous base, a pentose (five-carbon) sugar, and a phosphate group . Each nitrogenous base in a nucleotide is attached to a sugar molecule, which is attached to a phosphate group. Figure 2.21 A nucleotide is made up of three components: a nitrogenous base, a pentose sugar, and a phosphate group. DNA has a double-helical structure. It is composed of two strands, or polymers, of nucleotides. The strands are formed with bonds between phosphate and sugar groups of adjacent nucleotides. The strands are bonded to each other at their bases with hydrogen bonds, and the strands coil about each other along their length, hence the “double helix” description, which means a double spiral. Figure 2.22 Chemical structure of DNA, with colored label identifying the four bases as well as the phosphate and deoxyribose components of the backbone. (Chemical Structure of DNA by Madeleine Price Ball is CC0). The alternating sugar and phosphate groups lie on the outside of each strand, forming the backbone of the DNA. The nitrogenous bases are stacked in the interior, like the steps of a staircase, and these bases pair; the pairs are bound to each other by hydrogen bonds. The bases pair in such a way that the distance between the backbones of the two strands is the same all along the molecule. The rule is that nucleotide A pairs with nucleotide T, and G with C, see section 9.1 for more details. Living things are carbon-based because carbon plays such a prominent role in the chemistry of living things. The four covalent bonding positions of the carbon atom can give rise to a wide diversity of compounds with many functions, accounting for the importance of carbon in living things. Carbohydrates are a group of macromolecules that are a vital energy source for the cell, provide structural support to many organisms, and can be found on the surface of the cell as receptors or for cell recognition. Carbohydrates are classified as monosaccharides, disaccharides, and polysaccharides, depending on the number of monomers in the molecule. Lipids are a class of macromolecules that are nonpolar and hydrophobic in nature. Major types include fats and oils, waxes, phospholipids, and steroids. Fats and oils are a stored form of energy and can include triglycerides. Fats and oils are usually made up of fatty acids and glycerol. Proteins are a class of macromolecules that can perform a diverse range of functions for the cell. They help in metabolism by providing structural support and by acting as enzymes, carriers or as hormones. The building blocks of proteins are amino acids. Proteins are organized at four levels: primary, secondary, tertiary, and quaternary. Protein shape and function are intricately linked; any change in shape caused by changes in temperature, pH, or chemical exposure may lead to protein denaturation and a loss of function. Nucleic acids are molecules made up of repeating units of nucleotides that direct cellular activities such as cell division and protein synthesis. Each nucleotide is made up of a pentose sugar, a nitrogenous base, and a phosphate group. There are two types of nucleic acids: DNA and RNA. Exercises An example of a monosaccharide is ________. fructose glucose galactose all of the above Cellulose and starch are examples of ________. monosaccharides disaccharides lipids polysaccharides Phospholipids are important components of __________. the plasma membrane of cells the ring structure of steroids the waxy covering on leaves the double bond in hydrocarbon chains The monomers that make up proteins are called _________. nucleotides disaccharides amino acids&nbs chaperones Explain at least three functions that lipids serve in plants and/or animals. Explain what happens if even one amino acid is substituted for another in a polypeptide chain. Provide a specific example. Answers D D A C Fat serves as a valuable way for animals to store energy. It can also provide insulation. Phospholipids and steroids are important components of cell membranes. A change in gene sequence can lead to a different amino acid being added to a polypeptide chain instead of the normal one. This causes a change in protein structure and function. For example, in sickle cell anemia, the hemoglobin β chain has a single amino acid substitution. Because of this change, the disc-shaped red blood cells assume a crescent shape, which can result in serious health problems. amino acid: a monomer of a protein carbohydrate: a biological macromolecule in which the ratio of carbon to hydrogen to oxygen is 1:2:1; carbohydrates serve as energy sources and structural support in cells cellulose: a polysaccharide that makes up the cell walls of plants and provides structural support to the cell chitin: a type of carbohydrate that forms the outer skeleton of arthropods, such as insects and crustaceans, and the cell walls of fungi denaturation: the loss of shape in a protein as a result of changes in temperature, pH, or exposure to chemicals deoxyribonucleic acid (DNA): a double-stranded polymer of nucleotides that carries the hereditary information of the cell disaccharide: two sugar monomers that are linked together by a peptide bond enzyme: a catalyst in a biochemical reaction that is usually a complex or conjugated protein fat: a lipid molecule composed of three fatty acids and a glycerol (triglyceride) that typically exists in a solid form at room temperature glycogen: a storage carbohydrate in animals hormone: a chemical signaling molecule, usually a protein or steroid, secreted by an endocrine gland or group of endocrine cells; acts to control or regulate specific physiological processes lipids: a class of macromolecules that are nonpolar and insoluble in water macromolecule: a large molecule, often formed by polymerization of smaller monomers monosaccharide: a single unit or monomer of carbohydrates nucleic acid: a biological macromolecule that carries the genetic information of a cell and carries instructions for the functioning of the cell nucleotide: a monomer of nucleic acids; contains a pentose sugar, a phosphate group, and a nitrogenous base oil: an unsaturated fat that is a liquid at room temperature phospholipid: a major constituent of the membranes of cells; composed of two fatty acids and a phosphate group attached to the glycerol backbone polypeptide: a long chain of amino acids linked by peptide bonds polysaccharide: a long chain of monosaccharides; may be branched or unbranched protein: a biological macromolecule composed of one or more chains of amino acids ribonucleic acid (RNA): a single-stranded polymer of nucleotides that is involved in protein synthesis saturated fatty acid: a long-chain hydrocarbon with single covalent bonds in the carbon chain; the number of hydrogen atoms attached to the carbon skeleton is maximized starch: a storage carbohydrate in plants steroid: a type of lipid composed of four fused hydrocarbon rings trans-fat: a form of unsaturated fat with the hydrogen atoms neighboring the double bond across from each other rather than on the same side of the double bond triglyceride: a fat molecule; consists of three fatty acids linked to a glycerol molecule unsaturated fatty acid: a long-chain hydrocarbon that has one or more than one double bonds in the hydrocarbon chain References: Reference Ophardt, C. 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