

Chapter 2

Head and Tail

2.1 Fat Family: Fats and Fatty Acids

Oils and fats refer to a large and diverse group of compounds that do not easily dissolve in water. There is no strict distinction between oils and fats; fats usually refer to materials like wax, lard, and butter that are solid at room temperature, whereas oils like olive oil and fish oil are liquid. As is well known, butter can melt upon heating and olive oil solidify by freezing. Fats are just frozen oils.

The main part of a fat or an oil is a hydrocarbon moiety, typically a *long-chain hydrocarbon*, as shown in Fig. 2.1. Hydrocarbon chains can contain different numbers of carbon atoms, and the bonds between the carbon atoms can be single bonds (*saturated*) or double bonds (*unsaturated*). Hydrocarbons are said to be hydrophobic since they do not easily dissolve in water.

A hydrocarbon chain can be turned into a *fatty acid* by attaching a -COOH (carboxyl) group at the end as shown in Fig. 2.2a. The carboxyl group is said to be hydrophilic since it can be dissolved in water. Fatty acids therefore more easily dissolve in water than pure hydrocarbons. The fatty acids are the fundamental building blocks of all lipids in living matter. Plants and animals use a variety of fatty acids with chain lengths ranging from 2 up to 36. The most common chain lengths fall between 14 and 22. As we shall see in Sect. 15.1 this is likely to be controlled by the need for cells to have membranes with a certain thickness in order to properly function. Some bacteria have been found to have fatty-acid chains as long as 80.

There are various types of nomenclature for fatty acids: (i) trivial nomenclature, (ii) systematic nomenclature (IUPAC names), and (iii) lipid number nomenclature and Δ^x (delta- x) nomenclature used only for unsaturated fatty acids. The systematic name (IUPAC name) for fatty acids is derived from the name of its parent hydrocarbon by substitution of 'oic' for the final 'e.' For example oleic acid (see Fig. 2.3b) is called *cis*-9-octadecanoic acid because the parent hydrocarbon is *cis*-9-octadecane. The lipid number nomenclature, on the other hand, takes the form $\text{C:D}n_x$, where C is the number of carbon atoms in the fatty acid, and D is the number of double bonds in the fatty acid. The n_x part of the notation only denotes the position of the first double

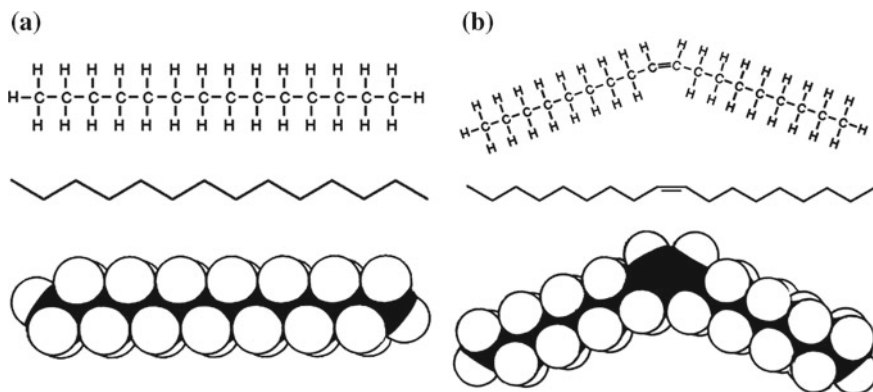


Fig. 2.1 Hydrocarbon chains shown in three different representations. *Top* all atoms and all bonds. *Middle* bonds between invisible carbon atoms placed at the vertices. *Bottom* space-filling models. **a** Saturated hydrocarbon chain with 14 carbon atoms. **b** Mono-unsaturated hydrocarbon chain with 18 carbon atoms. The double bond is here positioned in the middle of the chain

bond, i.e., n is a prefix and x is the number of the carbon atom that participates in the first double bond counting from the methyl terminal end of the chain (ω ; omega position). This nomenclature leads to the well-known ω -3 and ω -6 families of polyunsaturated fatty acids (see Sect. 16.1 for more details). Therefore, the lipid nomenclature for oleic acid is 18:1 n 9 (see Fig. 2.3). This notation can sometimes be ambiguous because some different fatty acids can have the same numbers (e.g., the *cis* and *trans* versions of oleic acid). Consequently, when ambiguity exists this notation is usually paired with the Δ^x term. In the Δ^x nomenclature each double bond is indicated by Δ^x . In this particular case the number for each double bond (located on the x th carbon) is counted from the carboxylic acid end of the molecule. In addition, the Δ^x term is preceded by *cis* or *trans* prefixes. For our oleic acid example the Δ^x nomenclature will be 18:1 *cis* Δ^9 while for linoleic acid this nomenclature will read 18:2 *cis*, *cis* $\Delta^9\Delta^{12}$. The trivial nomenclature often has its root in common language; e.g. particularly in chemistry it may come from historic usages in alchemy. The trivial name for 9(*cis*)-octadecanoic acid is oleic acid (because it is abundant in olive oil). Further examples of the systematic, lipid number, and trivial nomenclatures are given in Fig. 2.3.

It is most common to find chains with an even number of carbon atoms, although odd ones are found in rare cases. In animals and plants, most of the fatty-acid chains are unsaturated, most frequently with a single double bond (e.g., oleic acid shown in Fig. 2.2b) and in some cases with as many as six double bonds (docosahexaenoic acid, DHA) as shown in Fig. 2.2c. Unsaturated fatty acids with more than one double bond are called *poly-unsaturated*. Those with as many as five and six are called *super-unsaturated*. The occurrence of poly- and super-unsaturated fatty acids and how they are synthesized are described in Sect. 16.1.

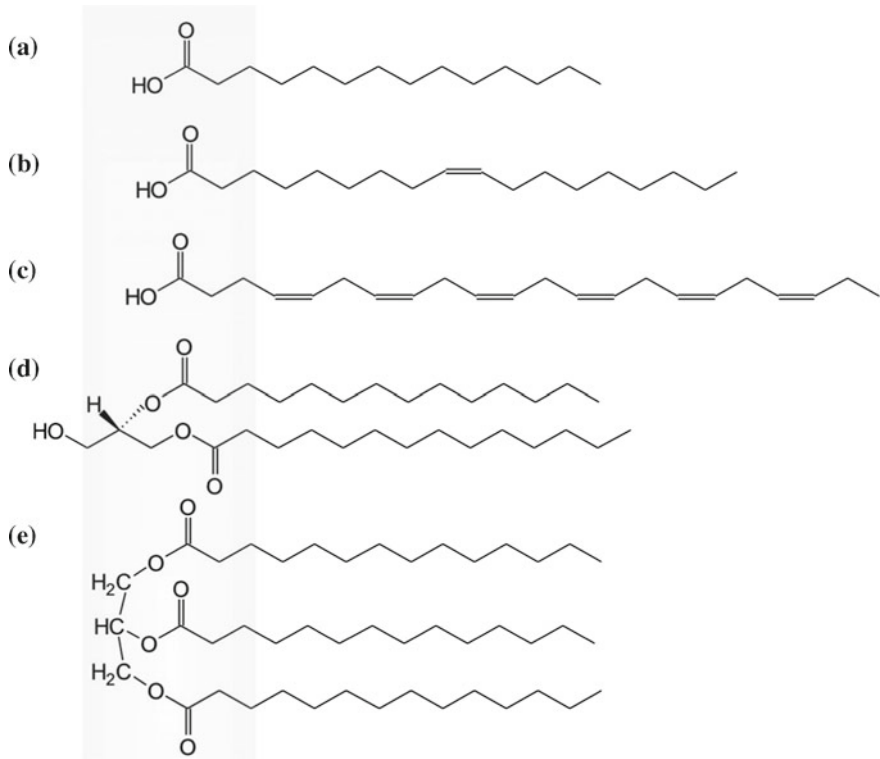


Fig. 2.2 Fats. The polar and aqueous region is shown to the *left* and the hydrophobic region to the *right*. The interfacial region is highlighted in grey. **a** Fatty acid (myristic acid, 14:0) corresponding to the hydrocarbon chain in Fig. 2.1a. **b** Oleic acid (18:1, with one double bond) corresponding to the hydrocarbon chain in Fig. 2.1b. **c** Docosahexaenoic acid (DHA) with six double bonds (22:6). **d** Di-acylglycerol (DAG) of myristic acid in (a). **e** Tri-acylglycerol (triglyceride) of myristic acid

LN#	Trivial	IUPAC	Chemical formula
Saturated fatty acids			
12:0	Lauric acid	Dodecanoic acid	$\text{CH}_3(\text{CH}_2)_{10}\text{COOH}$
14:0	Myristic acid	Tetradecanoic acid	$\text{CH}_3(\text{CH}_2)_{12}\text{COOH}$
16:0	Palmitic acid	Hexadecanoic acid	$\text{CH}_3(\text{CH}_2)_{14}\text{COOH}$
18:0	Stearic acid	Octadecanoic acid	$\text{CH}_3(\text{CH}_2)_{16}\text{COOH}$
20:0	Arachidic acid	Eicosanoic acid	$\text{CH}_3(\text{CH}_2)_{18}\text{COOH}$
22:0	Behenic acid	Docosanoic acid	$\text{CH}_3(\text{CH}_2)_{20}\text{COOH}$
24:0	Lignoceric acid	Tetracosanoic acid	$\text{CH}_3(\text{CH}_2)_{22}\text{COOH}$
Unsaturated fatty acids			
16:1n7	Palmitoleic acid	<i>cis</i> , 9-hexadecenoic acid	$\text{CH}_3(\text{CH}_2)_5\text{CH}=\text{CH}(\text{CH}_2)_7\text{COOH}$
18:1n9	Oleic acid	<i>cis</i> , 9-octadecenoic acid	$\text{CH}_3(\text{CH}_2)_7\text{CH}=\text{CH}(\text{CH}_2)_9\text{COOH}$
18:2n6	Linoleic acid	<i>cis</i> , <i>cis</i> , 9,12-octadecadienoic acid	$\text{CH}_3(\text{CH}_2)_4(\text{CH}=\text{CHCH}_2)_2(\text{CH}_2)_4\text{COOH}$
18:3n3	α -linolenic acid	<i>cis,cis,cis</i> , 9,12,15-octadecatrienoic acid	$\text{CH}_3(\text{CH}_2)_3(\text{CH}=\text{CHCH}_2)_3(\text{CH}_2)_1\text{COOH}$
18:3n6	γ -linolenic acid	<i>cis,cis,cis</i> , 6,9,12-octadecatrienoic acid	$\text{CH}_3(\text{CH}_2)_6(\text{CH}=\text{CHCH}_2)_3(\text{CH}_2)_1\text{COOH}$
20:4n6	Arachidonic acid	<i>cis,cis,cis,cis</i> , 5,8,11,14-eicosatetraenoic acid	$\text{CH}_3(\text{CH}_2)_4(\text{CH}=\text{CHCH}_2)_4(\text{CH}_2)_1\text{COOH}$
20:5n3	Eicosapentaenoic acid	<i>cis,cis,cis,cis,cis</i> 5,8,11,14,17-eicosapentaenoic acid	$\text{CH}_3(\text{CH}_2)_3(\text{CH}=\text{CHCH}_2)_5(\text{CH}_2)_1\text{COOH}$
22:6n3	Docosahexaenoic acid	<i>cis,cis,cis,cis,cis,cis</i> 4,7,10,13,16,19-docosahexenoic acid	$\text{CH}_3(\text{CH}_2)_2(\text{CH}=\text{CHCH}_2)_6(\text{CH}_2)_1\text{COOH}$
24:1n9	Nervonic acid	<i>cis</i> , 15-tetracosenoic acid	$\text{CH}_3(\text{CH}_2)_7\text{CH}=\text{CH}(\text{CH}_2)_{15}\text{COOH}$

*LN is the abbreviation for "lipid number" nomenclature.

Fig. 2.3 Nomenclature for fatty acids

Short-chain fatty acids can be produced by electrical discharges, e.g., lightening, out of inorganic compounds like carbon dioxide and methane. Intermediate- and long-chain fatty acids are believed only to be produced by biochemical synthesis in living organisms. Therefore, these fatty acids, along with amino acids, are taken as signs of life and are hence looked for in the exploration of extra-terrestrial life, e.g., in comets and on Mars.

Fatty acids are rarely found free in the cell, except when they transiently appear in the course of chemical reactions or are transported from cell to cell being attached to certain transporter proteins, so-called lipoproteins. Instead they are chemically linked to another group, e.g., *glycerol* as shown in Fig. 2.4 (left). Glycerol is an alcohol that can be esterified in up to three positions as illustrated in Fig. 2.2d, e in the case of a di-acylglycerol and a tri-acylglycerol derived from myristic acid. This process leads to the formation of a lipid molecule, in this case a *non-polar lipid*. The fatty-acid chains at the different positions can be different and most often they are, in triglycerides typically with a middle one that differs from the other two. Glycerol also acts as the *backbone* of *polar lipid* molecules as we shall return to below (cf. Sect. 2.2).

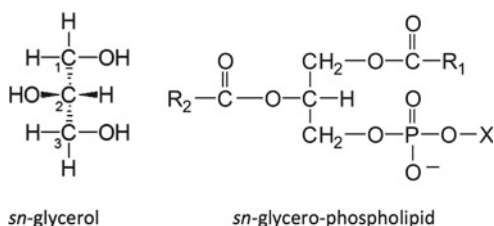
Di-acylglycerol (DAG) with two fatty acids is a key lipid molecule in certain signaling pathways which we shall describe in Sect. 19.3. Tri-acylglycerols are the typical storage lipid or fat, used for energy production, and saved in certain fat cells (adipocytes) and specialized fat (adipose) tissues.

2.2 The Polar Lipids—Both Head and Tail

Tri-acylglycerols are strongly hydrophobic which means that they cannot be dissolved in water. The affinity for water can be improved by replacing one of the fatty acids with a polar group. The resulting *polar lipid* then appears as a molecule with a *hydrophobic tail* and a *hydrophilic head* (see also Sect. 3.2).

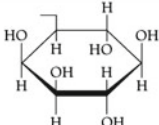
One strategy is to have a polar head with a phosphate group, in which case one has a *phospholipid*, a term that is used to classify phosphorus containing lipid molecules. This is a very generic term since there are different types of lipids species containing phosphorus. The term phospholipid in regular biochemistry or biology texts generally refers to glycerophospholipids as illustrated in Fig. 2.4 (right), although an important occurring sphingolipid named sphingomyelin (SM) also contains phosphorus (see below).

Fig. 2.4 *sn*-glycerol and *sn*-glycero-phospholipid



Glycero-phospholipids are abundant lipids in natural systems and they use the poly-alcohol glycerol as a backbone structure Fig. 2.4 (left). The backbone structure is a common characteristic of a given group of lipids. While glycerol itself is a symmetrical molecule, its carbon-2 becomes a chiral center when the 1- and 3-positions are not symmetrically substituted. It is therefore useful to define a prochiral *sn*-glycerol (*sn* = stereospecific numbering) in which the orientation of the 2-hydroxyl group and the numbering of the carbon are shown in Fig. 2.4 (left). In virtually all natural glycero-phospholipids the polar head group is attached to the 3-position of *sn*-glycerol. The polar head group contains a phosphate group that can be substituted by different compounds (*X*) through a covalent bond named phosphodiester (see Fig. 2.4 (right)). The most common chemical groups that are attached to the phosphate group are hydrogen, glycerol, serine, choline, ethanolamine, and myo-inositol generating phosphatidic acid, phosphatidylglycerol, phosphatidylserine, phosphatidylcholine, phosphatidylethanolamine, and phosphatidylinositol, respectively. These different polar head groups, which are abbreviated as PA, PG, PS, PC, PE, and PI, are shown in Fig. 2.5. While PC and PE lipids are neutral (zwitter-ionic), PS, PG, and PI lipids can be electrically charged. This difference has an important consequence for the capacity of the lipids, when incorporated into a lipid membrane, to bind proteins and drugs.

The different head groups generate different subfamilies of glycero-phospholipids, some of which are shown in Fig. 2.6. The simplest glycero-phospholipid is one with PA as a head group, from which all the other can be derived. For the particular case of PI-containing glycero-phospholipids, the polar head group can contain further phosphate substitutions in the myo-inositol group (called myo-inositol bi- or tri-phosphate). These lipids are important constituent of the inner leaflet of biological membranes and are claimed to be receptors of specific cytoplasmic proteins. The examples of phospholipids shown in Fig. 2.6a–g have two fatty-acid chains that are the same. The lipids in natural membranes usually contain two different chains and most often one of them is unsaturated. In the following chapters we shall for convenience represent polar lipids by the simple schematic illustration in Fig. 2.6i.

Substituent	Chemical formula*	Polar head group name	Ab ^{&}
hydrogen	-H	phosphatidic acid	PA
choline	-CH ₂ CH ₂ N(CH ₃) ₃ ⁺	phosphatidylcholine	PC
ethanolamine	-CH ₂ CH ₂ NH ₃ ⁺	phosphatidylethanolamine	PE
serine	-CH ₂ CH(NH ₃)COO ⁻	phosphatidylserine	PS
glycerol	-CH ₂ CH(OH)CH ₂ OH	phosphatidylglycerol	PG
myo-inositol		phosphatidylinositol	PI

*Chemical formula for the substituent linked to the phosphate group at position 3 of the glycerol moiety.

[&]Abbreviation for the polar head group nomenclature.

Fig. 2.5 Lipid polar head groups

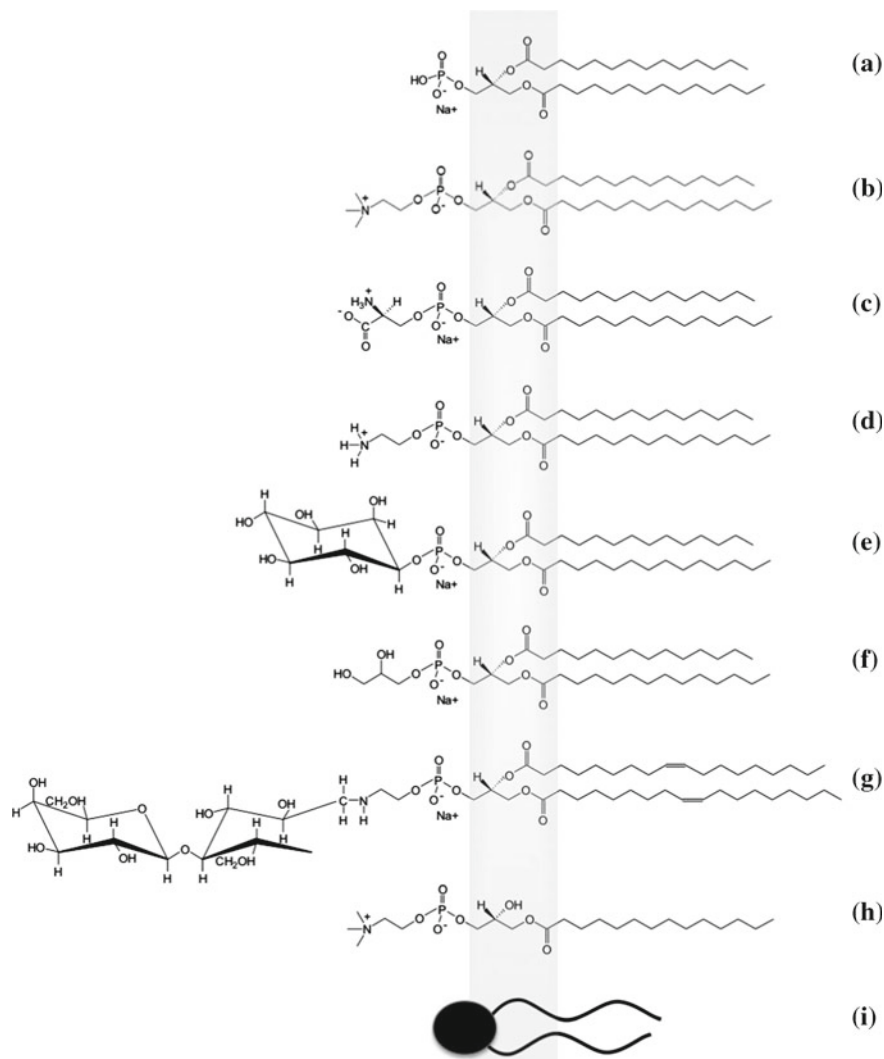


Fig. 2.6 Different polar glycerophospholipids. The polar and aqueous region is shown to the *left* and the hydrophobic region to the *right*. The interfacial region is highlighted in *grey*. **a** Di-myristoyl phosphatidic acid (PA). **b** Di-myristoyl phosphatidylcholine (PC). **c** Di-myristoyl phosphatidylserine (PS). **d** Di-myristoyl phosphatidylethanolamine (PE). **e** Di-myristoyl phosphatidylinositol (PI). **f** Di-myristoyl phosphatidylglycerol (PG). **g** A glycolipid. **h** A lysolipid with a palmitoyl chain. **i** Schematic representation of a polar lipid with a hydrophilic head group and a hydrophobic tail consisting of two hydrocarbon chains

The more accepted nomenclature for glycerophospholipids start with the glycerol backbone positions that are esterified by fatty acids, followed by the systematic name of the fatty acids, the term *sn*-glycerol, the glycerol position where the polar head group is linked, and the name of the polar head group. For example the name for the structure indicated in Fig. 2.6b is 1,2-ditetradecanoyl-*sn*-glycero-3-phosphocholine. Alternatively, the systematic name of the fatty acid can be replaced for its trivial name, e.g., 1,2-dimyristoyl-*sn*-glycero-3-phosphocholine for the same lipid structure indicated in Fig. 2.6b. In cases where the lipid molecule contains two different fatty acids residues, both must be mentioned. For example, the name for a glycerophospholipid containing PC as a polar head group and having palmitic and oleic acid residues in position 1 and 2 of the glycerol backbone is 1-hexadecanoyl, 2-*cis*, 9-octadecanoyl-*sn*-glycero-3-phosphocholine (or 1-palmitoyl-2-oleoyl-*sn*-glycero-3-phosphocholine).

An abbreviated nomenclature is for convenience often used to designate phospholipids such that the first letter of the trivial name of the fatty acids is followed by the polar head group abbreviation. For the particular case of the two lipid molecules referred to in the aforementioned examples the abbreviated names are DMPC (1,2-dimyristoyl-*sn*-glycero-3-phosphocholine) and POPC (1-palmitoyl, 2-oleoyl-*sn*-glycero-3-phosphocholine). Finally, another terminology can be found in the literature which uses the abbreviation of the polar head group followed by lipid number nomenclature for fatty acids. For example the lipid structure indicated in Fig. 2.6b is designated as PC(14:0/14:0).

When an ester bond is formed during the synthesis of a phospholipid, a water molecule is released. The reverse process, where an ester bond is broken, is referred to as *hydrolysis* (i.e., breaking water) or *lipolysis* (i.e., breaking lipids). Certain enzymes can perform lipolysis and we shall return to this in Chap. 18. The result of the lipolysis can be the formation of a so-called *lysolipid* which is a lipid missing one of the fatty-acid chains as shown in Fig. 2.6h.

The systematic nomenclature for the lyso-glycerophospholipids is similar to that of the diacyl case. For example the nomenclature for the lipid shown in Fig. 2.6h is 1-tetradecanoyl-*sn*-glycero-3-phosphocholine (or in the common nomenclature 1-myristoyl-2-hydroxy-*sn*-glycero-3-phosphocholine). This lipid can also be named as 14:0 lyso PC or 2-lysophosphatidylcholine (the 2-position here denotes the free hydroxyl group). These last two nomenclatures are somehow missing structural details of the lipid such as the position of the fatty acid linkage in the first case or the nature of the fatty acid in the second case.

Nature also uses another strategy to construct lipids with head and tail. Instead of using glycerol to bind the fatty acids, sphingosine, which is a long chain amine, can bind a fatty acid. While the prototypical backbone component of a sphingolipid is sphingosine (sphingenine, (2*S*,3*R*,4*E*)-2-amino-4-octadecene-1,3-diol), most sphingolipids preparations isolated from natural sources also contain significant proportions of other sphingoid bases that differ from sphingosine in hydrocarbon chain

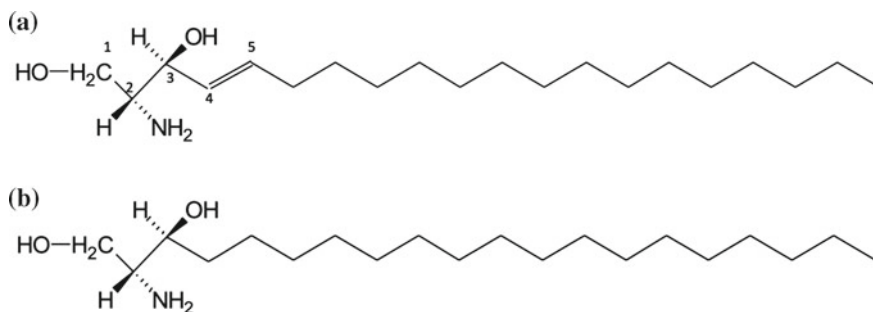


Fig. 2.7 Sphingosine (a) and sphinganine (b)

length, unsaturation at the 4-position, or hydroxylation at the 4-position. In Fig. 2.7 are shown the molecular structures of sphingosine and sphinganine (that lacks the Δ^4 unsaturation).

These structures can be modified by forming an amide bond with a fatty acid resulting in a large family of lipids based on sphingosine, which is called *sphingolipids*, examples of which are shown in Fig. 2.8. The simplest version of a sphingolipid is a lipid named *ceramide* (a N-acetylated sphingoid base). Its backbone is characteristic of sphingolipids. There is a series of different polar head groups linked to this structure. These chemical groups can be phosphate, phosphocholine, as well as various types of sugars resulting in very diverse molecular structures called *glycolipids*.

The structure of a naturally occurring ceramide is shown in Fig. 2.8a. Ceramide is a lipid present in the outermost layer of the skin (see Sect. 19.1) and also generated during programmed cell death (apoptosis), which is the topic dealt with in Sect. 19.4. The nomenclature for this particular ceramide is N-octadecanoyl-D-erythro-sphingosine, N-(octadecanoyl)-sphing-4-enine, or simply C18-ceramide. The prefix D-erythro refers to the class of diastereomers (stereoisomers that are not enantiomers, erythro and threo). Notice that ceramide residues, consisting of N-acylated sphingoid bases, are commonly named using either the trivial or the formal name of the coupled fatty acid group when the latter can be specified. Ceramides derived from a single sphingoid base are best named as the N-acyl derivatives of that base, while preparations containing more than one type of base but a single type of fatty acid residue can be named as an acyl ceramide. The IUPAC/IUB-recommended shorthand designation for a generic ceramide residue, Cer, is particularly useful in the designation of complex sphingolipids.

A range of different sphingolipids are represented in Fig. 2.8. As shown in the figure, substitutions in the hydroxyl group at the 1-position of the N-acylated sphingoid base lead to different lipids, such as sphingomyelin (SM) (containing PC as the glycerophospholipids), galactosyl-cerebroside, and the ganglioside GM₁. The galactosyl-cerebroside, which is a member of the subfamily of lipids called *cerebrosides* ubiquitous in myelin, is a natural precursor of a subfamily of lipids named *gangliosides*. Gangliosides are abundant in the nervous system and contain different

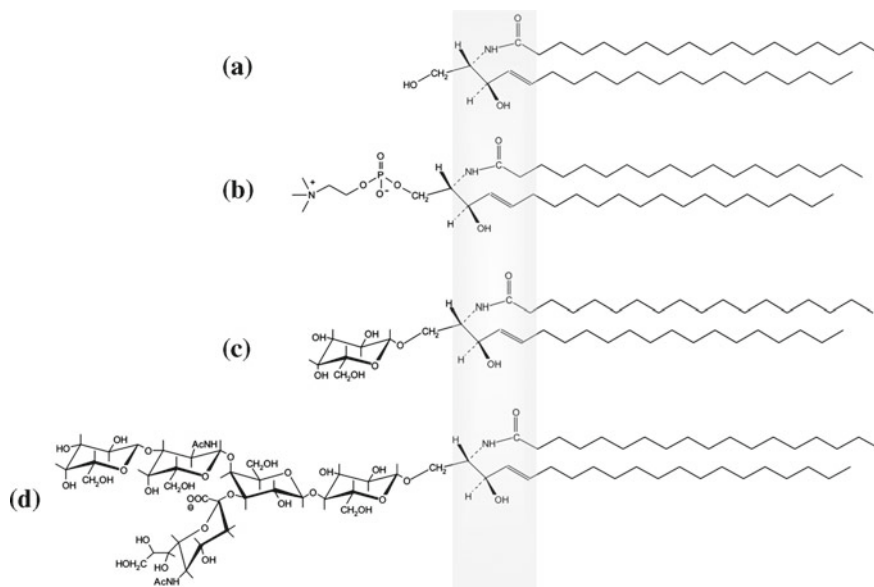


Fig. 2.8 Phospholipids based on sphingosine. The different molecules are not drawn to scale. **a** Ceramide. **b** Sphingomyelin (SM). **c** Cerebroside. **d** Ganglioside

amounts of sialic acid (N-acetyl-neuraminic acid) attached to the sugars in the polar head group showing a high compositional diversity. Examples are GM₃, GM₂, GM₁, GD_{1a}, GD_{1b}, and GT_{1b} containing respectively 3, 4, 5, 6, and 7 sugar residues. Glycosphingolipids are localized in the outer leaflet of the plasma membrane of all cells, where they help regulate cell-cell interactions, growth, and development. The carbohydrate chains of glycosphingolipids are antigenic (e.g., ABO blood group antigens). They also serve as cell-surface receptors for tetanus and cholera toxins (the latter interferes with G-protein signaling cascades). There are a number of inborn errors of sphingolipid metabolism, generally called sphingolipidoses, although individually rare, they are collectively a clinical concern in pediatrics, being a good reason to have a general understanding of their structure, nomenclature, and functions.

As mentioned above phospholipids can be broken down into their different parts by specific enzymes just like tri-acylglycerols can be hydrolyzed. These enzymes, which are called phospholipases, and their modes of action will be described in Chap. 18. Another type of enzyme, sphingomyelinase, can hydrolyze sphingomyelin.

Whereas the tri-acylglycerols are storage and fuel lipids, phospholipids and sphingolipids are structural and functional lipids. An enormous range of possible lipids can be perceived by varying, e.g., fatty-acid chain length, degree of saturation, polar head group, and type of glycosylation. It is hence not surprising that lipids are the chemically most diverse group of molecules in cells. The question naturally arises as to what is the reason and need for this richness and diversity?

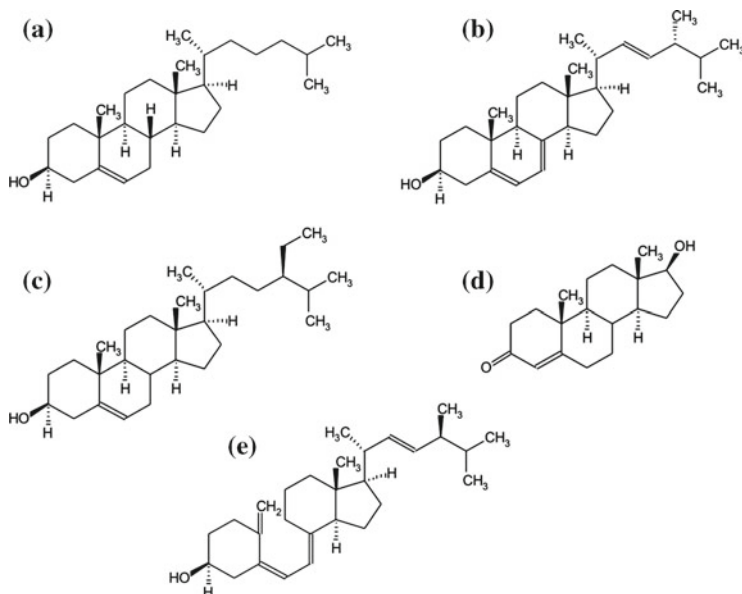


Fig. 2.9 Sterols related to cholesterol. **a** Cholesterol. **b** Ergosterol. **c** Sitosterol. **d** Testosterone (male sex hormone). **e** Vitamin D

2.3 Cholesterol—A Lipid of Its Own

Cholesterol is a lipid which is quite different from the phospholipids and sphingolipids we discussed above. Rather than having a fatty-acid chain as its hydrophobic part, cholesterol has a steroid ring structure, and a simple hydroxyl group ($-\text{OH}$) as its polar head. The steroid skeleton has a small hydrocarbon chain at the end. Hence cholesterol can be characterized as a lipid molecule with a bulky and stiff tail and a small head as shown in Fig. 2.9a. The molecular structure of cholesterol is very similar to that of bile salt, vitamin D, and sex hormones. Cholesterol is one of several members of the sterol family which play similar roles in different types of organisms, e.g., ergosterol in fungi and sitosterol in plants, cf. Fig. 2.9.

2.4 Strange Lipids

Some lipids appear to have rather strange structures which may suggest that they are useful for optimizing the physical properties of membranes that have to work under unusual conditions, for example at deep sea or in hot springs as described in Sect. 19.2. These lipids are either very bulky, very long, or based on ether chemistry rather than ester chemistry. The fact that we consider these lipids as strange is likely to reflect that

the current fashion of research is biased towards eukaryotic, in particular mammalian membranes, and that the world of e.g., the eubacteria and the archaeobacteria is much less explored.

In Fig. 2.10 are listed several lipids with unusual structures. *Cardiolipin* in Fig. 2.10a is basically a dimer lipid that has four fatty-acid chains and is found in the inner mitochondrial membrane, in plant chloroplast membranes, as well as in some bacterial membranes. Lipids based on ether bonding of fatty acids rather than ester bonding are frequently found in archaeobacterial membranes. As an example, a di-ether lipid with branched fatty-acid chains are shown in Fig. 2.10b. *Bolalipids* refer to a class of bipolar lipids, i.e., lipids with a polar head in both ends, which can span across a bacterial membrane. In Fig. 2.10c is shown an example of a bolalipid being a tetra-ether lipid which is a basic component of the membranes of halophilic archaeobacteria.

Finally, poly-isoprenoid lipids as illustrated in Fig. 2.10d are commonly associated with both prokaryotic and eukaryotic membranes and can act as lipid and sugar carriers.

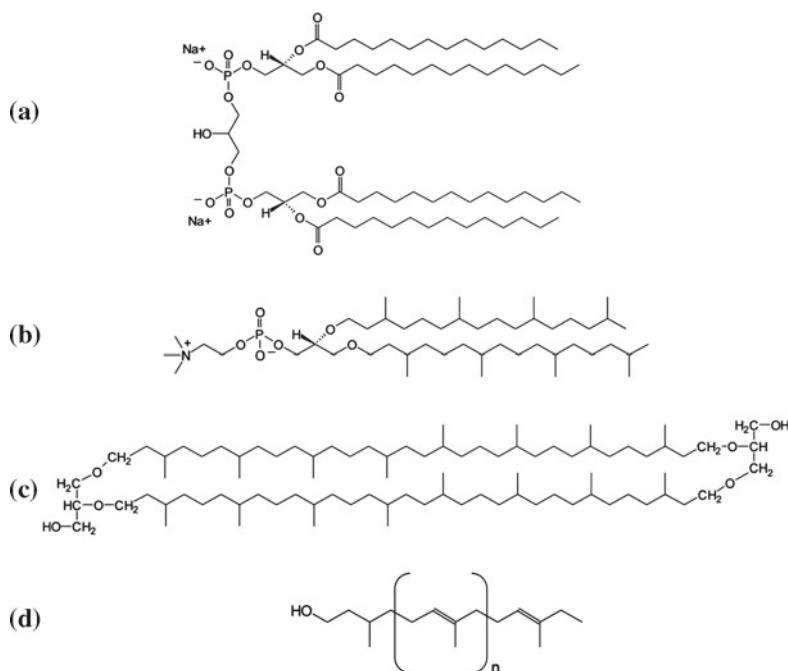


Fig. 2.10 A selection of strange lipids. **a** Cardiolipin. **b** Di-ether lipid. **c** Tetra-ether lipid (bolalipid, or di-biphytanyl-diglycerol-tetraether). **d** Poly-isoprenoid lipid

2.5 Lipid Composition of Membranes

As suggested by the description above, an enormous range of different lipids can be constructed. Obviously, Nature only exploits some of the possibilities, although the number of different lipid species found in a given kingdom of life and even within a single cell type is surprisingly large. Furthermore, a given type of cell or organism can only synthesize a limited range of lipids. For example human beings only produce few types of fats and lipids themselves. Most of the fats and lipids in our bodies come from the diet. We shall in Chap. 16 discuss this issue in the context of the fats of the brain and in the visual system.

Without making an attempt to give an overview of the lipid contents in different organisms and cell types, we quote some striking observations for mammalian plasma membranes that shall turn out to be relevant when discussing the physics of lipid membranes. It should be remarked, that there are characteristic differences between the lipid composition of plasma membranes and that of the various organelles.

Cholesterol is universally present in the plasma membranes of all animals (sitosterol in plants) in amounts ranging between 20–50 % of total lipids. In contrast, the organelle membranes contain very little, mitochondrial membranes less than 5 %, Golgi membranes about 8 %, and ER membranes around 10 %. In contrast, sterols are universally absent in the membranes of all prokaryotes. These striking numbers can be related to the role played by cholesterol in the evolution of higher organisms as described in Sect. 14.2.

The amount of charged lipids is about 10 % of the total lipid content in plasma membranes but there is a substantial variation in the ratio between PS and PI lipids. It is a remarkable observation that Nature only uses negatively charged and not positively charged lipids in membranes. It is generally found, that the longer the fatty-acid chain, the more double bonds are present. For example lipids with 18 carbon atoms have typically one double bond, those with 20 have four, and those with 22 have six. PC lipids have typically short chains, whereas SM often have very long chains. PE, PS, and PI lipids typically carry a high degree of unsaturation, whereas PC carry less.

There is a remarkable *lipid asymmetry* in the lipid composition of the two monolayers of the bilayer of the plasma membrane. Whereas SM, PC, cholesterol, and glycolipids are enriched in the outer monolayer, PS, PI, and PE are enriched in the inner layer.

LIFE - AS A MATTER OF FAT

Lipids in a Membrane Biophysics Perspective

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2016, XVII, 298 p., Hardcover

ISBN: 978-3-319-22613-2