

Biochemistry and Methodology of Lipids

EDITED BY

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and

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Foreword

"On the whole, such evidence as we possess supports the view that the lipins play an important part in the structure of the cell membrane, but it is not yet possible to dissociate the lipins from the other cell constituents, and attribute to them alone any specific properties associated with the cell."*

H. Maclean and I. Smedley Maclean

In seeking knowledge of a group of naturally occurring substances in living things it may be logical to inquire how many substances fall into our chosen category, what their structures are, in what definable parts of the organism they occur, and what functions they serve. To most of us the last is the most interesting question, and in many instances, certainly that of the lipids, the answers will depend in varying degree on the completeness and accuracy of the answers to the preceding questions. In this book the tools which are available to answer the preliminary questions and the methods by which they may be used are discussed. Their complexity and sophistication are considerable, all have been developed and applied only in the last twenty years, and each has its use and its own relevance in providing raw information which may help to answer the four types of question we ask.

None of these questions has been satisfactorily answered. Obviously the first can never be completely answered if only for the reasons that we are still discovering several thousand new species of living organisms every year, and even when all have been investigated completely, chemical mutations may still be expected to occur at a significant rate. Just how far we are from a complete answer is vividly shown by the fact that the first intimation of the existence of the class of phosphonolipids came less than ten years ago and of the chlorosulfolipids only in 1969. In regard to the second question, the chemical structures of some well-known lipids are still in doubt, and much remains to be done in the study of the intermolecular associations between lipids. As for the third question, the unsatisfactory nature of our knowledge of just where in the cell lipids occur, is well reflected in the current very lively controversy over the architecture of the cell membrane. Finally, there is the most interesting question—the function of lipids.

In the 1930s the burden of biochemical specificity clearly lay on proteins,

* *Lecithin and Allied Substances: The Lipins*, Longmans, Green & Co., London, 1927.

with their long chain length and multiplicity of residues of strikingly different properties. There was little cause to speculate on the possible specificity or informative content of the nucleic acids, for it was believed that they were, after all, only tetranucleotides. However, as the basis of type specificity in the pneumococci became better known, the polysaccharides appeared as if they might be contenders with the proteins for complexity and specificity of structure. Any general interest that the lipids were likely to have, appeared to arise from their physical properties, and it is interesting to recall that at that time considerable theoretical interest was shown, particularly by Needham, in the possible role of the liquid crystalline state in the organization of the cell.

Things have changed. The covalently linked protein and nucleic acid macromolecules are now the center of interest. Yet a further change is perhaps discernible. The advances of a science depend in large measure on the techniques available and the ease with which problems can be studied. Biochemistry is perhaps coming to the end of the first and easier phase, the study of covalently bound large and small molecules. The stage is set for the next qualitative change in our approach—the study of large, noncovalently bound complexes, in particular the associations of lipids and other molecules in the vital machinery of the cell. It is in this as yet vague and inchoate field that much of the future of biochemistry lies. It can be successfully entered only by those with a wide knowledge of the lipids, a group of diverse substances whose role in cell architecture and function may be comprehensible only through a knowledge of the loose, yet durable, structured associations they take part in with proteins. These associations, forming the membranes of the cell organelles, the cytoplasmic reticulum, and the cell itself, have a rich potentiality of imposing temporal and spatial order on metabolic processes at which we are only beginning to guess.

Those who organized the Australian Biochemical Society's summer school in lipid biochemistry and the editors of this book have provided a most valuable outline of the current knowledge and tools with which those venturing into this developing field may arm themselves. After using the book the reader should be in a better position to consider whether the forty year old statement appearing at the beginning of this Foreword, which was the last sentence of the Macleans' book, requires significant modification.

M. V. TRACEY

Preface

A summer school, sponsored by the Australian Biochemical Society, on the biochemistry and methodology of lipids was held at the Division of Food Research, Commonwealth Scientific and Industrial Research Organization (CSIRO), in February 1969. The eagerness to attend this school and the comments of the participants indicated that no suitable single book was available which would provide sufficient background to enable a worker, not versed in the field of lipids, to embark upon a program of experimental work. We have attempted to meet this need. With such a vast field of knowledge and techniques to summarize, inevitably some topics have not been covered. We hope, however, that the various authors have described the experimental techniques thoroughly and have given sufficient chemistry to provide an adequate background for these techniques and for biochemical and physiological studies of lipids. Furthermore, the authors have attempted to summarize the current knowledge concerning the biosynthesis and breakdown of most lipids and their roles in living cells. As space was limited there may be significant omissions, but we hope that the bibliography, especially the General Reading sections, will help to correct these shortcomings.

None of the chapters is intended to be a review of all the pertinent literature. Here again, however, the General Reading sections should serve as a guide and an introduction to the literature. We apologize to scientists whose work has not been referred to directly, and as editors we would personally welcome any constructive criticism of the book.

We are indebted to the Executive of CSIRO for permission to undertake this project; to Mr. M. V. Tracey, Chief of the Division of Food Research, for his help and encouragement; and to the many members of the staff of the division who helped in diverse ways during the preparation of the book. Our task as editors was made much easier as a result of the efforts of an Editorial Committee, whose members were Dr. D. G. Bishop, Dr. F. D. Collins, Mr. A. C. Fogerty, Dr. T. W. Scott, Professor P. K. Stumpf, and Mr. M. V. Tracey.

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1 The Nomenclature and Classification of Lipids

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1.1 INTRODUCTION

The scientist uses the word "lipid" to describe what the man in the street knows as a "fat" or an "oil." A dictionary definition (1)* of "lipid" is "Any of a group of substances that, in general, are soluble in ether, chloroform or other solvents for fats but are only sparingly soluble in water, that with protein and carbohydrates constitute the principal structural components of living cells, and that are considered to include fats, waxes, phosphatides, cerebrosides, and related and derived compounds and sometimes steroids and carotenoids—called also lipin, lipoid." Such a definition could be considered as a framework for this book. However, it avoids the issue of a rigorous scientific definition of "lipid," which, as Lovern (2) has pointed out, is difficult to make. The general term "lipid" is necessary because of the chemical complexity and the broad range of compounds involved. They cannot be defined as substances soluble in nonpolar solvents since many nonlipids are also soluble in these solvents, whereas some lipids are insoluble in such solvents. For example, sphingomyelin is insoluble in diethyl ether and most phospholipids are insoluble in acetone. In general, lipids are not

* Numbers in parentheses refer to items in the list of references at the end of each chapter.

soluble in water but the gangliosides are an exception. Considerations with regard to partition between water and water-immiscible solvents do not provide us with a suitable definition, as many nonlipids heavily favor the less polar phase.

Lipids can perhaps be satisfactorily defined as molecules, synthesized by biological systems, which have, as a major part of their structure, long aliphatic hydrocarbon chains that may be unbranched or branched, may form carbocyclic rings, and may contain unsaturated linkages. This molecular feature confers upon them the physical property of "fattiness" or "oiliness." Such a definition would include terpenes, some of which are important intermediates in steroid biosynthesis (Chapter 20) and which are closely related chemically to the carotenoids. The older terms "lipin" and "lipoid" have fallen out of general use. The word "fat" (or "oil" if the substance is a liquid at room temperature) is now confined by usage to the animal and plant triacylglycerols, which are major dietary components for animals and are important stores of energy in animals and seeds.

1.2 NOMENCLATURE

In the past there was no widely accepted systematic nomenclature for the lipids. Recently, however, the Combined Commission on Biochemical Nomenclature (CBN) of the International Union of Pure and Applied Chemistry (IUPAC) and the International Union of Biochemistry (IUB) has presented (3) tentative rules for the nomenclature of lipids. Rules for the nomenclature of steroids have also been recently published (4) by CBN, and both systems of nomenclature are used in this book wherever possible. The proposed rules for lipids are reproduced in Section 1.5, by kind permission of CBN.

1.3 CLASSIFICATION

Classification of lipids is difficult as they range chemically from simple hydrocarbons to steroids and complex amphiphilic lipids and functionally from storage fat to hormones and vitamins. Also the continuing discovery of unusual lipids, such as the "chlorosulfolipids" of the phytoflagellate, *Ochromonas danica* (5), necessitates continual modifications of existing systems of classification. The following classification, based essentially on chemical structure and derived from the earlier scheme of Bloor (6), is used in this book. Group A, the neutral lipids, differ from group B, the amphiphilic ($\alpha\mu\phi\iota$, both; $\phi\iota\lambda\epsilon\acute{\iota}\nu$, to love) lipids, in that the latter contain groups such as

phosphate esters, sugars, and amino acids which per se are not lipids but confer upon the amphiphilic lipid certain characteristic physical properties discussed in Chapter 3. The amphiphilic lipids are also commonly referred to as "polar lipids," but this term is not recommended as it contains an implied contradiction. Lipids are not polar compounds in the generally accepted sense of the word. They are also referred to as "complex lipids," but this term is not appropriate either, being applicable to some of the neutral lipids. The term "amphipathic" (*αμφι, both, of both kinds; πάθος, suffering*) is a possible alternative to "amphiphilic." The lipids classified in group C are chemically distinct from those of the first two groups by virtue of their ready oxidation and reduction, a property which is important to their function in biological systems.

A Classification of Lipids

A. Neutral Lipids

1. *Fatty acids*—long-chain, monocarboxylic acids.
2. *Glycerides*—compounds of glycerol containing only long hydrocarbon chains linked by acyl ester, saturated ether (*O*-alkyl), and vinyl ether (*O*-alk-1'-enyl) linkages.
3. *Waxes*—long-chain hydrocarbons; long-chain alcohols; esters of these alcohols and fatty acids.
4. *Estolides*—intermolecular lactones of hydroxy fatty acids.
5. *Carotenoids*—polyisoprenoid hydrocarbons, alcohols, epoxides, and carboxylic acids containing 40 carbon atoms. The isoprene residues are

linked tail-to-tail (i.e., $\begin{array}{c} \text{C} \\ | \\ \text{C}-\text{C}-\text{C} \cdots \text{C}-\text{C}-\text{C} \\ | \qquad \qquad | \\ \text{C} \qquad \qquad \text{C} \end{array}$) in the center of the molecule; this distinguishes them from the terpenoids, in which

all the linkages are head-to-tail (i.e., $\begin{array}{c} \text{C} \qquad \qquad \text{C} \\ | \qquad \qquad | \\ \text{C}-\text{C}-\text{C}-\text{C} \cdots \text{C}-\text{C}-\text{C}-\text{C} \\ | \qquad \qquad | \\ \text{C} \qquad \qquad \text{C} \end{array}$).

6. *Terpenoids*—polyisoprenoid compounds of varying carbon number, including the vitamin A group (which are derived from the carotenoids by splitting of the tail-to-tail linkage) and squalene, a hydrocarbon containing 30 carbon atoms which is an important intermediate in the biosynthesis of cholesterol (Chapter 20).
7. *Steroids*—alicyclic compounds, all of which have the same basic carbon skeleton as cyclopentanoperhydrophenanthrene (Chapter 23).

(Note: The term “neutral lipid” is preferred to “simple lipid” because of its widespread use and because some members of this group are not chemically simple. It must be remembered, however, that carboxylic acids in group A are not “neutral” and that some lipids in group B are “neutral”; for example, some of the glycolipids and zwitterionic lipids such as 3-*sn*-phosphatidylcholine (lecithin), which is uncharged under all physiological conditions.)

B. Amphiphilic Lipids

1. Glycerolipids

- 1a. *Phosphoglycerides*—any derivative of *sn*-glycero-3-phosphoric acid that contains at least one *O*-acyl or *O*-alkyl or *O*-alk-1'-enyl group. The last of these are known as *plasmalogens*.
- 1b. *Glycosylglycerides*—glycosides of diacylglycerol. Galactosides of diacylglycerol occur in all photosynthetic tissues and brain; galactosides, glucosides, and mannosides occur in bacteria.

2. Sphingolipids

- 2a. *Phosphosphingolipids*—phosphate esters of *N*-acyl sphinganine (ceramides), for example, sphingomyelin.
- 2b. *Glycosphingolipids*—glycosides of ceramides.
 - (i) Ceramide monoglycosides, which include
 - (a) *Cerebrosides*—glucosides or galactosides.
 - (b) *Sulfatides*—contain sulfate ester of galactose.
 - (ii) Ceramide oligoglycosides
 - (a) *Cytosides*—contain only simple sugars, for example, cytolipin H, a ceramide lactoside.
 - (b) *Globosides*—whose oligosaccharides contain, in addition to simple sugars, amino sugars and *N*-acetyl-amino sugars.
 - (c) *Gangliosides*—always contain acylated neuraminic acids (sialic acids) and may contain amino sugars. Always contain simple sugars.

(Note: Glycosides of sphinganine are called *psychosines*, that is, glycosphingolipids which have lost their fatty acid. Terms such as *phrenosine*, *cerebron*, *nervone*, and *oxynervone* were trivial names given to cerebroside preparations which contained predominantly one fatty acid. See Chapter 15.)

- 2c. *Glycophosphosphingolipids*—derivatives of ceramides containing both sugars and phosphate esters, for example, *phytoglycolipids* in plants (7).

(Note: The term *phospholipid* may be used for any lipid containing phosphorus, that is, classes 1a, 2a, and 2c.)

3. *Lipoamino acids* and *Lipopeptides*—compounds of fatty acids or long-chain alcohols with amino acids or peptides joined to them by ester or amide linkages, for example, *surfactin*, a fatty acid joined to a peptide by an amide linkage, from *Bacillus subtilis* (8), and an ornithine-containing lipid from nonsulfur purple bacteria (9). Although amino acid esters of 3-*sn*-phosphatidylglycerol are also referred to as lipoamino acids, they are more properly classified as phosphoglycerides (class B.1a).
4. Other *Glycolipids*—a group of glycolipids which are neither glycerolipids nor sphingolipids. They occur principally in mycobacteria, and as lipopolysaccharides in cell envelopes of Gram-negative bacteria.

C. Redox Lipids

1. *Quinones*—include the *ubiquinones*, the *plastoquinones*, and the vitamin K group (*phyloquinones* and *menaquinones*).
2. *Chromans*—include the *tocopherols*, the *tocotrienols*, and the *ubichromenols* (chromenes). All redox lipids have polyisoprenoid chains in addition to their redox structure.

1.4 FORMULAE OF SOME LIPIDS OF BIOLOGICAL INTEREST

1.4a Neutral Lipids

(i) Fatty acids are the long-chain compounds of widest occurrence in lipids and are probably the class of greatest physiological interest. Rules for their nomenclature have been laid down by IUPAC (10), and they should always be numbered with the carboxyl group as C-1. Tables 1.1 through 1.5 list some fatty acids of biological interest.

(ii) Acylglycerols are esters of fatty acids and glycerol. There are three types: monoacyl, diacyl, and triacyl, the third group being found in the greatest amount. Fats and oils can contain a large number of triacylglycerols; the total number of possible different triacylglycerols with n different fatty

TABLE 1.1
Straight-Chain Saturated Fatty Acids, $C_nH_{2n+1}COOH$

Shorthand designation	Recommended name	Alternative name	Systematic name	Formula	Occurrence
1:0	Formic		Methanoic	HCOOH	
2:0	Acetic		Ethanoic	CH ₃ COOH	
3:0	Propionic		Propanoic	CH ₃ CH ₂ COOH	
4:0	Butyric		Butanoic	CH ₃ (CH ₂) ₂ COOH	Butter
5:0	Valeric		Pentanoic	CH ₃ (CH ₂) ₃ COOH	
6:0	Hexanoic			CH ₃ (CH ₂) ₄ COOH	Butter, palm oil, coconut oil
7:0	Heptanoic			CH ₃ (CH ₂) ₅ COOH	
8:0	Octanoic			CH ₃ (CH ₂) ₆ COOH	Butter, palm oil, coconut oil
9:0	Nonanoic	Pelargonic		CH ₃ (CH ₂) ₇ COOH	
10:0	Decanoic			CH ₃ (CH ₂) ₈ COOH	Butter, whale oil, coconut oil
11:0	Undecanoic			CH ₃ (CH ₂) ₉ COOH	
12:0	Lauric		Dodecanoic	CH ₃ (CH ₂) ₁₀ COOH	Seed oils of Lauraceae
13:0	Tridecanoic			CH ₃ (CH ₂) ₁₁ COOH	

14:0	Myristic		Tetradecanoic	$\text{CH}_3(\text{CH}_2)_{12}\text{COOH}$	Widespread
15:0	Pentadecanoic			$\text{CH}_3(\text{CH}_2)_{13}\text{COOH}$	
16:0	Palmitic		Hexadecanoic	$\text{CH}_3(\text{CH}_2)_{14}\text{COOH}$	Widespread
17:0	Heptadecanoic	Margaric		$\text{CH}_3(\text{CH}_2)_{15}\text{COOH}$	
18:0	Stearic		Octadecanoic	$\text{CH}_3(\text{CH}_2)_{16}\text{COOH}$	Widespread
19:0	Nonadecanoic			$\text{CH}_3(\text{CH}_2)_{17}\text{COOH}$	
20:0	Eicosanoic	Arachidic		$\text{CH}_3(\text{CH}_2)_{18}\text{COOH}$	Seed oils, fish oils
21:0	Heneicosanoic			$\text{CH}_3(\text{CH}_2)_{19}\text{COOH}$	
22:0	Docosanoic	Behenic		$\text{CH}_3(\text{CH}_2)_{20}\text{COOH}$	Seed oils
24:0	Tetracosanoic	Lignoceric		$\text{CH}_3(\text{CH}_2)_{22}\text{COOH}$	Seed oils
26:0	Hexacosanoic	Cerotic		$\text{CH}_3(\text{CH}_2)_{24}\text{COOH}$	Waxes

^a Short-chain fatty acids are included in the list for completeness and for their importance in lipid metabolism, although, according to the definition given earlier in this chapter, they are not lipids.

^b Systematic names are used for fatty acids containing more than 26 carbon atoms, which occur principally in waxes.

^c The names "caproic" (6:0), "caprylic" (8:0), and "capric" (10:0) are no longer used because of possible confusion between them.

^d Systematic names are used for substituted acids except 1:0 to 5:0 (9).

TABLE 1.2
Some Straight-Chain Monenoic Fatty Acids, $C_nH_{2n-1}COOH$

Shorthand designation	Recommended name	Alternative name	Systematic name	Formula	Occurrence
12:1	<i>cis</i> -9-Dodecenoic	Lauroleic		$CH_3CH_2CH=CH(CH_2)_7COOH$	Butter
12:1	<i>cis</i> -5-Dodecenoic			$CH_3(CH_2)_5CH=CH(CH_2)_5COOH$	Fish oils
14:1	<i>cis</i> -9-Tetradecenoic	Myristoleic		$CH_3(CH_2)_9CH=CH(CH_2)_4COOH$	Widespread
16:1	<i>cis</i> -9-Hexadecenoic	Palmitoleic		$CH_3(CH_2)_5CH=CH(CH_2)_9COOH$	Widespread
18:1	Oleic		<i>cis</i> -9-Octadecenoic	$CH_3(CH_2)_7CH=CH(CH_2)_9COOH$	Widespread
18:1	Elaidic		<i>trans</i> -9-Octadecenoic	$CH_3(CH_2)_7CH=CH(CH_2)_9COOH$	Ruminants
18:1	<i>cis</i> -6-Octadecenoic	Petroselinic		$CH_3(CH_2)_{10}CH=CH(CH_2)_4COOH$	Parsley seeds
18:1	<i>trans</i> -6-Octadecenoic	Petroselaic		$CH_3(CH_2)_5CH=CH(CH_2)_9COOH$	Widespread
18:1	<i>cis</i> -11-Octadecenoic	Vaccenic		$CH_3(CH_2)_8CH=CH(CH_2)_7COOH$	Fish oils
20:1	<i>cis</i> -9-Eicosenoic	Gadoleic		$CH_3(CH_2)_9CH=CH(CH_2)_9COOH$	Fish oils
22:1	<i>cis</i> -11-Docosenoic	Cetoleic		$CH_3(CH_2)_9CH=CH(CH_2)_9COOH$	Seed oils of
22:1	Erucic		<i>cis</i> -13-Docosenoic	$CH_3(CH_2)_7CH=CH(CH_2)_{11}COOH$	Cruciferae
24:1	<i>cis</i> -15-Tetracosenoic	Nervonic		$CH_3(CH_2)_7CH=CH(CH_2)_{13}COOH$	Fish oils, brain

TABLE 1.3
Some Straight-Chain Polyenoic Fatty Acids, $C_nH_{2n-x}COOH$

Shorthand designation	Recommended name	Alternative name	Systematic name	Formula	Occurrence
18:2	Linoleic		<i>cis</i> -9, <i>cis</i> -12-Octadecadienoic	$CH_3(CH_2)_4CH=CHCH_2CH=CH(CH_2)_7COOH$	Widespread
18:2	<i>trans</i> -9, <i>trans</i> -12-Octadecadienoic				
18:3	Linolenic	Linelaidd	<i>cis</i> -9, <i>cis</i> -12, <i>cis</i> -15-Octadecatrienoic	$CH_3(CH_2)_4CH=CHCH_2CH=CH(CH_2)_7COOH$	Ruminants
18:3	<i>trans</i> -9, <i>trans</i> -12, <i>trans</i> -15-Octadecatrienoic			$CH_3CH_2CH=CHCH_2CH=CHCH_2CH=CH(CH_2)_7COOH$	Widespread
18:3	α -Eleostearic		<i>cis</i> -9, <i>trans</i> -11, <i>trans</i> -13-Octadecatrienoic	$CH_3CH_2CH=CHCH_2CH=CHCH_2CH=CH(CH_2)_7COOH$	
18:3	β -Eleostearic		<i>trans</i> -9, <i>trans</i> -11, <i>trans</i> -13-Octadecatrienoic	$CH_3(CH_2)_3CH=CHCH=CHCH=CH(CH_2)_7COOH$	Some plants
				$CH_3(CH_2)_3CH=CHCH=CHCH=CH(CH_2)_7COOH$	

TABLE 1.3 (continued)

Shorthand designation	Recommended name	Alternative name	Systematic name	Formula	Occurrence
18:3	<i>cis</i> -6, <i>cis</i> -9, <i>cis</i> -12-Octadecatrienoic	γ -Linolenic		$\text{CH}_3(\text{CH}_2)_4\text{CH}=\text{CHCH}_2\text{CH}=\text{CHCH}_2-\text{CH}=\text{CH}(\text{CH}_2)_4\text{COOH}$	
18:3	<i>cis</i> -9, <i>trans</i> -11, <i>cis</i> -13-Octadecatrienoic	Punicic		$\text{CH}_3(\text{CH}_2)_3\text{CH}=\text{CHCH}=\text{CHCH}=\text{CH}(\text{CH}_2)_7\text{COOH}$	Some plants
20:3	<i>cis</i> -8, <i>cis</i> -11, <i>cis</i> -14-Eicosatrienoic	Homo- γ -linolenic		$\text{CH}_3(\text{CH}_2)_7\text{CH}=\text{CHCH}_2\text{CH}=\text{CHCH}_2-\text{CH}=\text{CH}(\text{CH}_2)_3\text{COOH}$	Animals
20:4	Arachidonic		<i>cis</i> -5, <i>cis</i> -8, <i>cis</i> -11, <i>cis</i> -14-Eicosatetraenoic	$\text{CH}_3(\text{CH}_2)_4\text{CH}=\text{CHCH}_2\text{CH}=\text{CHCH}_2\text{CH}=\text{CHCH}_2-\text{CH}=\text{CH}(\text{CH}_2)_3\text{COOH}$	Widespread in animals
20:4	<i>cis</i> -8, <i>cis</i> -11, <i>cis</i> -14, <i>cis</i> -17-Eicosatetraenoic			$\text{CH}_3\text{CH}_2\text{CH}=\text{CHCH}_2\text{CH}=\text{CHCH}_2\text{CH}=\text{CHCH}_2-\text{CH}=\text{CH}(\text{CH}_2)_6\text{COOH}$	Animals
20:5, 22:5, and 22:6 acids occur widely in fish oils.					