Lipids and Lipid Polymers in Higher Plants

Edited by

M. Tevini and H. K. Lichtenthaler

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With 136 Figures

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Preface

This book contains a number of papers dealing with the main topics of a Symposium on "Lipids and Lipid Polymers in Higher Plants", held in July 1976 at the Botanical Institute of the University of Karlsruhe. The symposium was organized by Professors E. Heinz, H.K. Lichtenthaler, H.K. Mangold, and M. Tevini. The sponsorship by the *Deutsche Forschungsgemeinschaft* and the *Erwin-Riesch-Stiftung* is gratefully acknowledged.

The intention of the Symposium was to bring together in one place scientists working in very different fields of plant lipids, such as fatty acids, glycolipids, phospholipids, prenyllipids, sterols, and lipid polymers. The emphasis was placed on biosynthesis, distribution, function, and physiology of the various higher plant lipids and their role in biomembranes and epidermal cell walls.

By combining the major contributions in this book, we hope to give all plant scientists access to the recent developments in biochemistry and physiology of plant lipid metabolism. The editors are very grateful to the contributors, who have taken great care to present up-to-date reviews.

Karlsruhe, May 1977

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CHAPTER 1

Functional Organization of Biomembranes

P. SITTE

A. Introduction

Lipidology is, to a large extent, also membranology. The intracellular lipid species [34] can be classified either as storage lipids, represented chiefly by the neutral and apolar triglycerides that form spherical inclusions in plasmatic phases, or as amphiphilic structural lipids, which form extended, sheetlike structures, and which are, by and large, identical with biomembrane lipids. Biomembranes comprise up to 30% of a cell's dry weight. In energy-transducing organelles, biomembranes amount to still higher percentages.

In earlier times, when the 'elementary' membranes within the cell could neither be seen nor analyzed due to the lack of suitable methods, membrane phenomena seemed to play only a limited part in the cell's life. Since the advent of the electron microscope and of cell fractionation techniques the situation has changed drastically. Today it proves difficult to find any important phenomenon in cell biology *not* correlated with membrane action. A few, more obvious functions are: separation of metabolically different compartments; intracellular storage; specific and unidirectional translocation of certain compounds within the cell, and, consequently, a powerful regulation of metabolic activities; vectorial electron transport and ATP synthesis; impulse transmission; control of cellular movements up to the precise control of muscular contraction; translation, in the case of proteins to be secreted; at least certain aspects of DNA replication; segregation of genetic material in protocytes as well as in some more primitive eucytes; hormone action in animals and plants; phytochrome-mediated control of different plant cell activities; cell-cell recognition, communication, cooperation (and, therefore, some basic aspects of sexuality, development, and differentiation, cancer, and memory)—everywhere we find biomembranes involved directly or indirectly in vital events.

In fact, membranology has become a vast field, with hundreds of pertinent publications appearing every year (for recent reviews see, e.g., [12, 13, 16, 18, 35, 38, 39, 40, 58, 60, 82, 86, 88, 98, 111, 116, 124, 137, 156, 157, 159]). Therefore, just a few basic problems can be considered here. In particular, the following questions will be discussed:

1. What is the most general function that biomembranes serve in the living cell and how well are they fitted to serve that function?

2. How do biomembranes develop, and how do they become differentiated? Is there de novo synthesis of elementary membranes, or is there, in a certain sense, genetic continuity?

3. Which general factors govern size and shape of cells and subcellular

compartments; and to what extent is molecular self-assembly of lipid phases involved?

4. What do we really know about the molecular architecture of biomembranes?

As will be seen, biomembranes are the most important lipid-containing structures of living cells, and it is the lipid moiety of these membranes that is of particular importance.

B. Membrane Functions

I. Membrane Diversity

Every contemporary illustration of cell fine structure [21, 56, 79, 118] reminds one of the astonishing multiplicity of biomembranes in average eucytes (eukaryotic cells).

The different membranes as seen from such illustration or electron micrographs differ in thickness and spatial arrangement, as well as in their associated enzymatic activities and in their lipid composition. They also vary in their respective protein content, which in turn is strictly correlated with buoyant density, as shown in Figure 1 for some lipid carrier particles of blood [127]. Thus, the several membrane species can be separated by isopyknic centrifugation (Fig. 2) on the basis of differing protein contents. Differences in protein content are also reflected by particle density as observable on freeze-etch fracture faces of biomembranes [11, 83] (cf. Fig. 13).

Nevertheless, these membranes also have many properties in common. The generic term elementary membrane has been introduced to designate all of them—irrespective of their particular composition and function [141].

What *functions* can be served by elementary membranes?

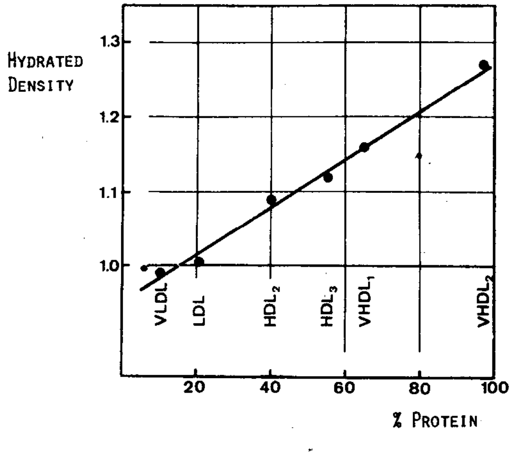

Fig. 1. Buoyant densities of lipoprotein particles from blood in correlation with their respective protein content [127]. *VLDL:* very low density lipoprotein; *LDL:* low density lipoprotein; *HDL* and *VHDL:* high density and very high density lipoprotein

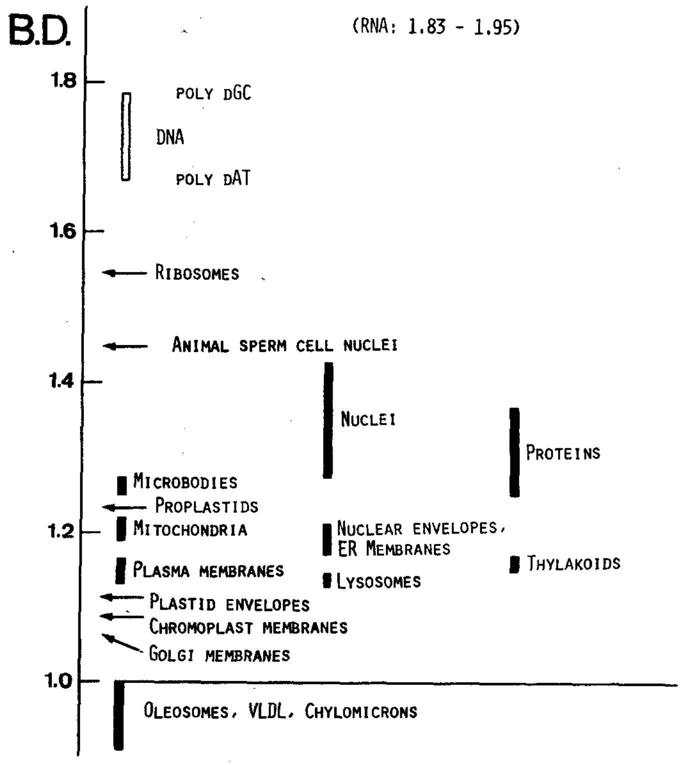

Fig. 2. Buoyant densities (*B.D.*) of some subcellular structural units, according to data in literature and own results. Author is indebted to Prof. Dr. W.W. Franke for collecting many of these data

They normally contain or carry enzymes [23, 89] and often lipophilic pigments also. Plasma membranes in particular act as chemical antennae [26, 27, 46, 50, 101], since many chemical stimuli, as mediated by hormones, transmitters [147, 152], mating substances [73, 92], or antigens, cannot penetrate the cell and are thus perceived to be at the cell surface. Yet the different *internal* elementary membranes must also possess surface specificities for membrane-membrane recognition as, for example, during membrane flow processes [28, 44, 45, 99, 109, 112, 113, 126, 132, 133, 160, 161]. Membranes also often take part in *cellular movements*. This is best demonstrated by the segregation of genetic material as mediated by the plasma membrane in bacteria [81, 110]. In eucells, membranes may serve as microtubule organizing centers or provide attraction points for contracting microfilaments (see, e.g., [4, 30, 103]).

Permeand selection in *membrane transport* often exhibits high specificity similar to enzymatic reactions [8, 9, 57, 77, 102, 141, 165]. However, as Berlin has shown [7], membrane permeases possess specificities complementary to the ones of intracellular enzymes. For example, amino acid permeases are stereospecific for the L-α-configuration, whereas the different aminoacyl-tRNA-synthetases exhibit high specificities for the different R-groups.

The fact that cellular *energy transformation* also depends, to a large part, on specialized membranes has only become clear in recent years [2, 33, 95, 96, 97, 121].

II. Membranes as Barriers

If one tries to reduce the different membrane functions just mentioned to a common denominator, one basic property common to all of them stands out, namely, the ability to impair free diffusion. Membranes principally act as barriers, both around the living cell and within it. The significance of compartmentation of the cellular interior by cytomembranes is to be seen mainly in the *separation* of certain metabolic events [93]. In higher plants, which, in contrast to higher animals, do not possess central organs for excretion, the single cell has to confine its own wastes away from metabolically active compartments [142]. In fortunate cases, such a local excrction can be seen in electron micrographs (Fig. 3).

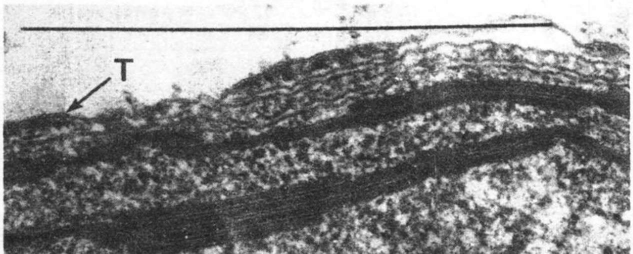

Fig. 3. Thylakoids filled with osmiophilic (possibly polyphenolic) substance. Petals of *Forsythia viridissima*, mesophyll. Plasma membrane (*P*) and tonoplast membrane (*T*) partly resolved as trilaminate unit membranes. Bar: 1 µm

Membranes can produce or maintain steep *concentration gradients* and (electro-)chemical potentials only because of their restricted permeability. Such potentials are of decisive importance in metabolism [93]. Even a few leaks, such as those produced by ionophores, channel-forming macrocyclic antibiotics, polyene antibiotics, or by complement action, inevitably kill the affected cell.

After some recent discoveries, we are just beginning to realize the role of compartmentation in the complex demands of cellular life. That steep proton concentration gradients are essential for ATP synthesis by thylakoids and mitochondrial inner membranes [95, 96, 97, 121] seems now to be generally agreed upon [52, 61, 62, 75, 115, 151, 163, 164]. Yet some totally different events are also under the control of pH gradients, as, for example, ion transport through plasma membranes [6, 155], the so-called overspill in photosynthetic light reaction as well as certain essential steps in dark reactions [3], and even lactose permease activity in *Escherichia coli* [135]. The electrochemical potential as generated by the expulsion of sodium ions from the cell is used not only in impulse transmission by nerves and muscles, but also for an active inward transport of amino acids and sugars by epithelial cells [63, 71]. Finally, there are indications of a regulation of intracellular membrane fusion during membrane flow by the local concentration of calcium ions [113, 126], which in turn might be under the control of smooth endoplasmic reticulum (ER)—as in striated muscle—or of mitochondria.

III. Lipids and Permeability

Many membrane functions require the high specificity of both intrinsic and extrinsic proteins. Yet whenever the membranes are to act as barriers against a free exchange of material, lipids must be considered: Their presence ensures restricted permeability [158]. Insulating membranes such as those of nerve myelin are particularly rich in lipids. Furthermore, the permeability properties of a given membrane depend on the kinds of lipid molecules involved. In general, it can be stated that, for an elementary membrane, the higher the content of long-chain, saturated fatty acids, the lower the permeability. Cholesterol has a similar effect, which, by means of hydrophobic interaction, causes a marked condensation effect within lipid films [29]. It is perhaps noteworthy, in this context, that plasma membranes exhibit higher percentages of both cholesterol and sphingomyelin than do the internal cytomembranes. Sphingolipids possess two saturated hydrocarbon chains whereas glycerophosphatides normally carry an *un*saturated chain in the β position.

No membrane is perfect: there is always a certain degree of leakyness, which has been termed passive permeability. This rather unspecific process is adequately described by the lipid-filter theory [158]. In Figure 4, several polar and apolar permeands are shown: among the polar molecules, urea (60 daltons) is for many biomembranes the largest permeand. Apolar particles, on the other hand, may penetrate even when they are many times larger.

The lipid-filter theory created the belief that biomembranes must contain a continuous fluid lipid sheet [108, 158]. In fact, artificial lipid layers exhibit permeability properties quite similar to those of elementary membranes [150].