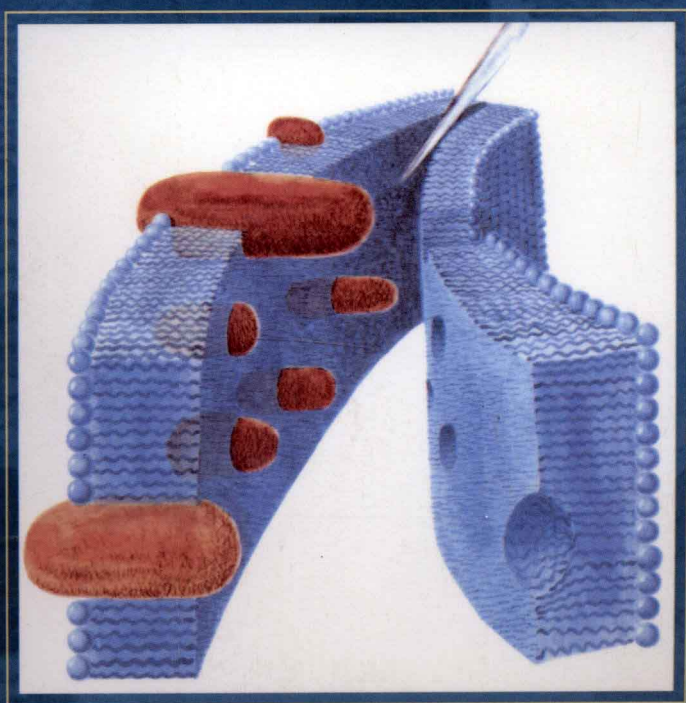


# MICELLES, MONOLAYERS, and BIOMEMBRANES

*Malcolm N. Jones*

*Dennis Chapman*



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**MALCOLM N. JONES**

School of Biological Sciences  
University of Manchester  
Manchester, United Kingdom

**DENNIS CHAPMAN**

Royal Free Hospital School of Medicine  
London, United Kingdom



 **WILEY-LISS**

A JOHN WILEY & SONS, INC., PUBLICATION

New York • Chichester • Brisbane • Toronto • Singapore

**Address All Inquiries to the Publisher**  
**Wiley-Liss, Inc., 605 Third Avenue, New York, NY 10158-0012**

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**Printed in the United States of America**

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#### **Library of Congress Cataloging-in-Publication Data**

Jones, Malcolm N.

Micelles, monolayers, and biomembranes / by Malcolm N. Jones and  
Dennis Chapman.

p. cm.

Includes bibliographical references and index.

ISBN 0-471-56139-8. — ISBN 0-471-30596-0 (pbk.)

1. Membranes (Biology) 2. Hydrophobic surfaces. 3. Micelles.  
4. Monomolecular films. I. Chapman, Dennis, 1927- . II. Title.

QH601.J614 1994

574.87'5—dc20

94-30352

CIP

**The text of this book is printed on acid-free paper.**

# MICELLES, MONOLAYERS, AND BIOMEMBRANES

# PREFACE

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The objective in writing this book was to attempt to present in an up-to-date single volume those phenomena that arise as a consequence of hydrophobicity. The formation of monolayers, micelles, liposomes, and natural membranes (biomembranes) is to varying degrees a direct consequence of the amphipathic nature of their constituent parts, and the properties of such systems are intimately affected by hydrophobic interactions. In bringing together a body of information on the nature of such systems we hope that the reader will be able to appreciate and to understand the immense importance of amphipathic molecules and their role in determining the structure and properties of monolayer, bilayer, and biomembrane systems.

We are of course conscious of the enormous size of the monolayer, micelle, and biomembrane fields; whole volumes could be devoted to each one of these areas. We have therefore had to be selective in the topics we have chosen to discuss. Such choices are difficult to make, and subjective. Inevitably we may have omitted areas that some will think might also have been included. We have nevertheless endeavoured to give a broad and up-to-date coverage of the fields where amphipathic molecules are involved. Thus we have also included chapters where such topics as protein translocation, chaperones, and biomembrane dynamics are discussed, as these are also directly related to the amphipathic character of these systems. We have included further reading suggestions in some of the chapters as well as specific references.

While the book assumes some knowledge of both physical chemistry and biochemistry/biology, we have attempted as far as possible to give appropriate introductory information, although of necessity this is brief in parts. We hope the book will be of general interest to third-year students of both the physical and biological sciences and to those researchers who wish to be introduced to

the manifestations of hydrophobic interactions. Finally, we would like to express our appreciation to our typists, Miss Lynne Smith in Manchester and Mrs. Laks Sinha in London, for word processing technically difficult manuscripts, and to Mrs. Christine Hall in London for general assistance. Special thanks are also due to Mr. Steven Wilkinson and his father, Dr. Alan E. Wilkinson, who have redrawn in a unified fashion, using computer graphics, all the figures taken from the literature. Their work has greatly enhanced the appearance of the book. We also thank Mr. Jason W. Birkett in the Department of Chemistry at Manchester for drawing the organic formulae in Chapter 5.

MALCOLM N. JONES  
DENNIS CHAPMAN

*Manchester and London, 1994*

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# CHAPTER 1

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## THE CHEMISTRY AND ROLE OF AMPHIPATHIC MOLECULES

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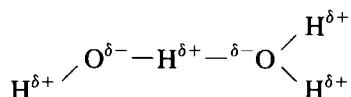
### 1.1. OCCURRENCE OF AMPHIPATHICITY AT THE MOLECULAR LEVEL

The occurrence of molecules having both hydrophobic and hydrophilic moieties in chemical combination gives rise to an extensive range of phenomena and structural patterns, the importance of which can hardly be underestimated in both the physical and life sciences. The widespread use of soaps and detergents, the stabilization of foams and emulsions in the processing of beverages and foodstuffs, the stabilization of particulate dispersions such as paints, and the secondary recovery of oil from porous rock beds are all processes that depend on the use of molecules with a dual character, i.e., amphipathic molecules. It is almost inconceivable to consider the existence of life forms and living processes without amphipathic molecules. From the stabilization of globular proteins to the formation of complex organelles and membranous structures, amphipathicity plays a vital role in facilitating the development of the structural features necessary for the evolution and maintenance of life processes.

The simultaneous existence of chemical entities having an affinity and an antipathy for water within the same molecule is the pivot around which amphipathicity revolves. In terms of chemical structure, amphipathic molecules have hydrophobic alkyl, acyl, or aromatic groups in combination with polar and/or ionizing groups with hydrophilic character. It is the need to satisfy these conflicting characteristics and minimize the energy of the system that gives rise to the formation of a host of complex structural features involving the coming together of the hydrophobic residues in the bulk phase to form aggregated

structures such as micelles, and that leads to interfacial phenomena such as the formation of monolayers, bilayers, and related vesicular structures and, of course, the all-important existence of the biological membrane.

The manifestation of amphipathicity requires the existence of what is the most unique liquid on the planet: water. Water has been called the “matrix of life” (A. Szent-Gyorgy, 1957), and it is water’s unique physical properties, together with its abundance, that has enabled life to be evolved in its present form. Table 1.1 shows some of the physical properties of water compared with those of three other common liquids, methanol, benzene, and *n*-hexane. Perhaps the most unusual feature of water is that it is a liquid at all at ambient temperatures. The “hydrides” of nitrogen and sulphur—ammonia (NH<sub>3</sub>, molecular mass 17.03) and hydrogen sulphide (H<sub>2</sub>S, molecular mass 34.08)—have melting points of  $-77.7^{\circ}\text{C}$  and  $-85.5^{\circ}\text{C}$ , respectively, and are gaseous at room temperatures. Thus water has a high melting point and a high boiling point for its molecular mass; it also has an exceptionally high heat capacity, high surface tension, and high relative permittivity. These characteristics are a consequence of the structure of water in the solid and liquid states, which in turn arise from the phenomenon of hydrogen bonding. The charge displacement between the electronegative oxygen atom and the hydrogen atoms, which may be illustrated as follows:



gives rise to a linear bond between two water molecules with an energy in the range  $20\text{--}35 \text{ kJ mol}^{-1}$ . The interaction energy between water molecules arising

**TABLE 1.1. Physical Properties of Some Common Liquids**

Property	Water	Methanol	Benzene	<i>n</i> -Hexane
Molecular mass ( $\text{g mole}^{-1}$ )	18.02	32.04	78.12	86.18
Melting point (K)	273	175	279	178
Boiling point (K)	373	338	353	342
Enthalpy of fusion ( $\Delta H_{\text{fus}}$ , $\text{kJ mol}^{-1}$ )	5.98	2.57	9.9	13.1
Enthalpy of evaporation ( $\Delta H_{\text{evap}}$ , $\text{kJ mol}^{-1}$ )	40.5	35.2	30.8	28.9
$\Delta H_{\text{fus}}/\Delta H_{\text{evap}}$	6.8	13.7	3.1	2.2
Heat capacity, $C_p$ ( $\text{J.mol}^{-1} \text{K}^{-1}$ )	75.2	2.61	10.6	16.8
Density at $20^{\circ}\text{C}$ ( $\text{g cm}^{-3}$ )	0.998	0.791	0.879	0.660
Surface tension at $20^{\circ}\text{C}$ ( $\text{mNm}^{-1}$ )	72.8	22.6	28.9	18.4
Relative permittivity ( $20^{\circ}\text{C}$ )	80.1	32.6	2.28	1.89

Data from Weast (1976).

from the hydrogen bond contribution leads to the formation of aggregates of water molecules from dimers to large molecular clusters in which the molecules inside the clusters can form up to four hydrogen bonds with their surrounding neighbors. In this four-point-charge model, due to Bjerrum, the four surrounding molecules were orientated tetrahedrally, but it is known that the tetrahedral is not quite regular. In the solid state at low pressures (ice I), the four-coordinated structure is a very open one with a large amount of empty space. A consequence of this is that ice is very sensitive to pressure and eight other crystalline modifications exist as well as the normal ice I. When ice melts, the structural features of ice I remain to a considerable degree, and it is the partial breakdown of the ice-like structure between 0°C and 4°C that gives rise to the phenomenon of maximum density at 4°C. However, in liquid water molecular clusters still remain above 4°C. The low latent heat of fusion (compared with, e.g., benzene and *n*-hexane, Table 1.1) and the high latent heat of evaporation reflect the retention of ice-like structure on melting and the breakdown of residual hydrogen bonding on boiling, respectively. The dynamics of the formation and breakdown of the molecular clusters in the liquid state led to them being called "flickering clusters"; their lifetime is of the order of  $10^{-10}$  to  $10^{-11}$  seconds (Frank and Wen, 1957).

Hydrophobicity and hydrophilicity are manifestations of the unique properties of water, and in particular of two essential features, the open hydrogen-bonded structure and the high relative permittivity, respectively. The existence of molecular clusters in the liquid state means that depending on the nature of the solute, the clusters can either be broken down or enhanced. The ease with which many ionic salts dissolve in water, in contrast to their insolubility in organic solvents, relates to the relative ease of separation of the ions due to the high permittivity of water and follows directly from the inverse relationship between the force between ions of opposite charge and the relative permittivity of the medium (Coulomb's Law). In solution, the ions are hydrated by water molecules so that the nearest-neighbor water molecules are largely immobilized by direct ion-dipole interactions. However, surrounding the immobilized water layer is a region of water that differs in structure from bulk water, and for many common salts—e.g., the alkali halides—this region has less ice-like character than bulk water. Such ions are "structure-breaking" and destabilize the flickering clusters, which is manifest in decreases in the partial molal heat capacities of many electrolyte solutions; if there is less "ice-likeness," then less heat is required to raise the temperature of the solution. If, however, we turn to tetraalkylammonium salts, the situation is very different—the apparent molal heat capacities are now larger than expected by up to about  $500 \text{ J K}^{-1} \text{ mol}^{-1}$  for, e.g., tetrabutylammonium bromide. This enhanced heat capacity can be regarded as arising from an increase in ice-likeness or a "structure-making" effect due to the inserting of the nonpolar alkyl groups into the water structure. It is the structure-making effect of nonpolar groups in water that is at the root of the hydrophobic effect (see, e.g., Ben Naim, 1980; Tanford, 1973).

The Frank and Wen model of flickering clusters in water and the increasing ice-likeness of water induced by nonpolar solutes was addressed in statistical mechanical terms by Némethy and Scheraga (1962). They considered a distribution of the water molecules over five possible energy levels from the unhydrogen-bonded state to water molecules in the center of a flickering cluster forming four hydrogen bonds. Molecules at the surface of flickering clusters could form one, two, or three hydrogen bonds. When the energy of the hydrogen bond and the free volume of system are made adjustable parameters, many of the physical properties of liquid water can be accounted for and the structure-forming effect of nonpolar solutes can be quantified as shown in Table 1.2, where the mole fractions of water molecules in the different hydrogen-bonded states are given. For aliphatic and aromatic solutes, the mole fraction of water molecules that are forming four hydrogen bonds is increased by 88% and 65%, respectively, relative to the value in pure water.

The structure-forming effect of nonpolar solutes should not be taken to imply that aliphatic and aromatic groups interact favorably with water; their low solubilities and their adsorption at the aqueous-air interface are manifestations of their antipathy for water, and the intermolecular forces between nonpolar solutes are not particularly strong—in fact fluorocarbons, the most hydrophobic materials, have very weak intermolecular forces. The hydrophobic effect thus relates not to the affinity of nonpolar solutes for themselves (like-like interactions) but to the strong interactions between water molecules, as expressed by Hartley (1936), due largely to hydrogen bonding, which results in nonpolar solutes being “squeezed out” of liquid water because to accommodate them in the water requires reorientation of the water structure with a concomitant decrease in entropy. It is for this reason that the term *hydrophobic bonding*, with the implication of interaction between hydrophobic groups, is to some degree ill chosen to describe the hydrophobic effect. Thermodynamically, the increase in entropy resulting from the breakdown of structured regions around nonpolar residues when they are removed from contact with water molecules makes a major contribution to the lowering of the Gibbs energy of the system and in this sense is the “driving force” behind the hydrophobic effect.

**TABLE 1.2. Mole Fractions of Water Molecules in Different Hydrogen-Bonded States at 30°C**

Energy State <sup>a</sup>	Pure Water	Aliphatic Solute	Aromatic Solute
0	0.318	0.237	0.256
1	0.237	0.133	0.144
2	0.044	0.183	0.198
3	0.194	0.056	0.060
4	0.207	0.389	0.341

From the model of Némethy and Scheraga (1962).

<sup>a</sup>Number of hydrogen bonds formed.

## 1.2. TYPES OF AMPHIPATHIC MOLECULES

Amphipathic molecules are ubiquitous in biological systems, and the large surface-to-volume ratio of cells, plasma membranes, cell organelles, and other subcellular structures means that a relatively large proportion of the molecules present are located at interfaces between different bulk phases. A necessary thermodynamic requirement for the existence of a stable interface is that the Gibbs energy of formation of the interface must be positive. If this were not so and the Gibbs energy of formation of the interface were negative, it would grow spontaneously, with the result that one phase would disperse into another. Thus work must be done to extend an interface. The work is done against the interfacial tension and is given by the product of interfacial tension and the change in area. The presence of amphipathic molecules at an interface lowers the interfacial tension and hence reduces the amount of work required to extend it.

In biological systems, numerous processes occur at interfaces, and particularly those associated with membranes such as active, facilitated, and passive transport of substrates and the formation of adenosine triphosphate (ATP) from adenosine diphosphate (ADP) by oxidative phosphorylation and photosynthesis. The stability of biological membranes and the functional systems associated with them depend on the amphipathic nature of their components, specifically the membrane lipids, proteins and glycoproteins. But before discussing the role of amphipathicity in membrane structure, it is appropriate to consider the most important types of amphipathic molecules.

### 1.2.1. Synthetic Surfactants

Synthetic surfactants are used extensively in the study of biological membranes in order to solubilize membrane components prior to their separation for analysis of composition and/or to get them in a form suitable for manipulation, for example, in the isolation and reconstitution of membrane transport proteins and membrane receptors (Jones et al., 1987). These applications will be discussed in more detail in later chapters. The present discussion is restricted to the types of synthetic surfactants that are extensively used for these purposes.

Surfactants are the active constituents in detergent formulations and generally consist of one or two hydrophobic moieties, typically alkyl chains covalently linked to an ionic or hydrophilic polar headgroup. They can thus be classified in terms of their headgroup as anionic (negatively charged headgroup), cationic (positively charged headgroup), zwitterionic (a headgroup carrying a positive and a negative charge), or nonionic (uncharged but polar headgroup).

Single alkyl chain surfactants are the most frequently used. Figure 1.1 shows the structures of some synthetic surfactants commonly used in membrane studies and their acronyms and/or trade names. The most significant parameter for a surfactant is the concentration at which it forms micelles in solution (see

**Anionic Surfactants**

$C_{12} H_{25} O SO_3^-$	$Na^+$	sodium $n$ -dodecylsulphate (SDS)
$C_{12} H_{25} SO_3^-$	$Na^+$	sodium $n$ -dodecylsulphonate
$C_{12} H_{25} \text{---} \text{C}_6\text{H}_4 \text{---} SO_3^-$	$Na^+$	sodium $n$ -dodecylbenzene sulphonate

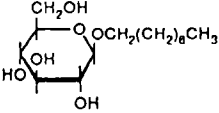
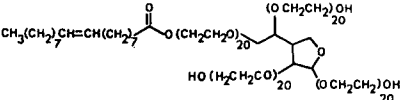
**Cationic Surfactants**

$C_{16} H_{31} N^+(CH_3)_3$	$Br^-$	$n$ -hexadecyltrimethylammonium bromide CTAB
$C_{12} H_{25} N^+(CH_3)_3$	$Br^-$	$n$ -dodecyltrimethylammonium bromide (DTAB)
$C_{12} H_{25} \text{---} N^+ \text{---} \text{C}_5\text{H}_5$	$Cl^-$	$n$ -dodecylpyridinium chloride

**Zwitterionic Surfactants**

$C_{12} H_{25} \text{---} N^+(CH_3)_2 \text{---} CH_2 CH_2 CO_2^-$	$n$ -dodecyl-N-betaine
$C_{14} H_{29} \text{---} N^+(CH_3)_2 \text{---} CH_2 CH_2 CH_2 SO_3^-$	N-tetradecyl [N,N-dimethyl-3-ammonia-1-propane sulphonate (Zwittergent 3-14)]

**Nonionic Surfactants**

$CH_3 \text{---} C(CH_3)_2 \text{---} CH_2 \text{---} C(CH_3)_2 \text{---} \text{C}_6\text{H}_4 \text{---} (OCH_2CH_2)_n OH$	Lubrol PX (polyethylene glycol $n$ -dodecanol) $n = 9 - 10$
	Octyl glucoside (OBG) ( $n$ -octyl- $\beta$ -D-glucopyranoside)
	Triton X-100 (polyethyleneglycol p- <i>t</i> -octylphenol) $n = 9 - 10$
	Tween 80 (polyethylene glycol sorbitan monooleate)

**Fig. 1.1.** Structures of some synthetic surfactants.