Biophysics

Roland Glaser

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An Introduction

Second Edition

Springer

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ISBN 978-3-642-25211-2 e-ISBN 978-3-642-25212-9
DOI 10.1007/978-3-642-25212-9
Springer Heidelberg Dordrecht London New York

Library of Congress Control Number: 2012936486

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

"Was war also das Leben? Es war Wärme, das Wärmeprodukt formerhaltender Bestandlosigkeit, ein Fieber der Materie, von welchem der Prozeß unaufhörlicher Zersetzung und Wiederherstellung unhaltbar verwickelt, unhaltbar kunstreich aufgebauter Eiweißmolekel begleitet war. Es war das Sein des eigentlich Nicht-sein-Könnenden, des nur in diesem verschränkten und fiebrigen Prozeß von Zerfall und Erneuerung mit süß-schmerzlich-genauer Not auf dem Punkte des Seins Balancierenden. Es war nicht materiell und es war nicht Geist. Es war etwas zwischen beidem, ein Phänomen, getragen von Materie, gleich dem Regenbogen auf dem Wasserfall und gleich der Flamme."

Thomas Mann, Der Zauberberg

"What then was life? It was warmth, the warmth generated by a form-preserving instability, a fever of matter, which accompanied the process of ceaseless decay and repair of albumen molecules that were too impossibly complicated, too impossibly ingenious in structure. It was the existence of the actually impossible-to-exist, of a half-sweet, half-painful balancing, or scarcely balancing, in this restricted and feverish process of decay and renewal, upon the point of existence. It was not matter and it was not spirit, but something between the two, a phenomenon conveyed by matter, like the rainbow on the waterfall, and like the flame." *(Translated by H.T. Lowe-Porter, Penguin Books, 1985, pp. 275–276)*

Thomas Mann, The Magic Mountain

Preface to the Second English Edition

More than a decennium has passed since I finished the first English edition of this textbook – a long time for a rapidly developing science! A mass of original publications as well as reviews and books for each of the addressed topics can always be found on the website of the "Web of Knowledge." Consequently, a full revision of all chapters was necessary, and a number of new results and topics had to be included.

The long time it took in writing this textbook, starting from the first German edition in 1971, reflects an important period of development of biophysics as a modern scientific discipline. It was extremely fascinating to not only observe the progress in biophysics but also to follow the ups and downs of the crucial aspects of its development. At first radiation biophysics dominates. Later one biocybernetics, discussion about entropy and negentropy, extended Onsager matrices of coupled flux equations, dissipative structures, types of kinetic catastrophes, the paradox of spontaneous protein folding, etc. were discussed in extension. All of these approaches and ideas have eventually been well fitted into the complex system of biophysics more or less according to their real importance.

It was not easy to decide on what really should be included in such an introductory textbook, what should be the length of the corresponding sections, how should the plethora of new facts and relations be arranged, and what a student should essentially know to be able to understand the complex framework of biophysics. The author is aware of the subjective nature of these decisions.

At present, biophysical research is mainly focused on molecular structures and processes. This has indeed proved important and helpful in the preparation of this textbook, as new results of molecular biophysics could be included in various sections of this edition. It should be noted, however, that the molecules are embedded in a definite medium. Osmotic and Donnan-osmotic effects control the biological reactions and functions of these molecules. Therefore, the basic figures of "classical" thermodynamics should not be forgotten. The Nernst equation as well as all other basic equations derived by famous physicists – Planck, Fick, Donnan, etc. – still valid and indispensable even in modern research. Therefore, these are maintained in some sections and, in some parts, are compared with and are strongly oriented to actual applications.

The increasing environmental consciousness worldwide during the last decades also enforces an extensive research on possible influences of physical parameters, such as electromagnetic fields and radiation, on biological systems and human health. This has been discussed in the chapter on environment biophysics, leading to its extension and new structuring.

The enormous upturn of biological systems theory, caused by the abundance of analytical data as well as new methods of data storage and management, thanks to new computer techniques, required a full revision of the last part of this textbook. Earlier graphical methods to analyze data of compartment analyses are outdated and, hence, replaced by corresponding computer softwares. At the same time, some other approaches, for example, the "classical" graph theory of Leonard Euler, have become the new actuality in the age of fast computer techniques. This strongly promotes biological network analysis.

This new edition could not have been possible without the help of friends and colleagues. I would especially like to thank Peter Hegemann and Andreas Herrmann for their help with the chapters on molecular biophysics; Andreas Möglich for revising the sections on light; and Edda Klipp, Hanspeter Herzel, and Werner Ebeling for their help with the theoretical chapters. I also had many discussions and e-mail exchanges on problems of electrical properties of tissues and cells with my former coworker Jan Gimsa. The section of radiobiology has been written in collaboration with Jürgen Kiefer. I wish to express my deepest gratitude to all of them.

Last, but not least, I would like to thank Springer, especially Jutta Lindenborn for her support and, particularly, for her tireless efforts in the preparation of this new edition. The proposal to use color prints, I think, makes the figures more suggestive and comprehensible.

Berlin
March 2012

Roland Glaser

Preface to the First English Edition

When I started teaching biophysics to biology students at the Friedrich Schiller University of Jena in 1965, the questions arose: What actually is biophysics? What should I teach? Only one thing seemed to be clear to me: biophysics is neither "physics for biologists" nor "physical methods applied to biology," but a modern field of science leading to new approaches of our understanding of biological functions.

Rashevsky's book *Mathematical Biophysics* (1960), the classical approaches of Ludwig von Bertalanffy (1968), as well as the excellent book by Katchalsky and Curran *Nonequilibrium Thermodynamics in Biophysics* (1965) showed me new ways of looking at biological processes. Thus, I came to the conclusion that it would be worthwhile trying to integrate all these various physical and physicochemical approaches to biological problems into a new discipline called "biophysics." The first German edition of this textbook, published in 1971, was developed from these considerations.

Meanwhile, I had moved from Jena to the Humboldt University in Berlin, where I organized courses for biologists specializing in biophysics. The idea was: Why should only physicists find their way to biophysics? Why not help biologists overcome the "activation energy" barrier of mathematics and physics and discover this fascinating discipline?

In Berlin, a special group was established (1970) in the Department of Biology with the aim of teaching biophysics. This led to a full university degree course of biophysics, which has developed successfully and attracts an increasing number of students today.

Consequently, my coworkers and I had the responsibility of organizing not only introductory courses to biophysics for biology students but also advanced courses in molecular biophysics, biomechanics, membrane biophysics, bioelectrochemistry, environmental biophysics, and various aspects of theoretical biophysics.

The evolution of this textbook in the following years was the result of these courses. Innumerable discussions with students, colleagues, and friends led to continuous refinement and modification of the contents of this book, resulting in a second, third, and, in 1996, a fourth German edition. New topics were added and others updated or even deleted. The only sentences that remained unchanged were those of Thomas Mann at the beginning of the Preface.

The philosophy of this book is that biophysics is not simply a collection of physical approaches to biology but a defined discipline with its own network of ideas and approaches, spanning all hierarchical levels of biological organization. The paradigm of a holistic view of biological functions, where the biological system is not simply the sum of its molecular components but is rather their functional integration, seems to be the main concept of biophysics.

While it is easier to realize such an integrated view in a “one-man book,” this has, of course, the disadvantage that the knowledge and experience of many specialists cannot be incorporated. However, to a certain degree, this problem was compensated by discussions with colleagues and friends and by their continuous support over a period of more than three decades. Further problems are the selection of the topics to be included in the book and the emphasis placed on the different aspects, avoiding the underestimation of others. Although I have tried to balance the selection and emphasis of topics by looking at the development of biophysics over the last three decades, I am not sure that I have succeeded. Even if this is the case, this book will at least help to answer the question: What is biophysics? It provides a solid introduction to biophysics. For further reading, books and reviews are recommended at the end of each chapter. The extensive index at the end of the book ensures an easy orientation and will enable this book to be used as a reference work.

As mentioned above, this book is written primarily for biologists and biophysicists with a background in biology. Therefore, some basic knowledge of biology is required, but less knowledge of physics and mathematics is needed. It should encourage biologists to enter the field of biophysics and stimulate further research. The German editions have shown that physicists also can profit from reading this book.

This first English edition is not just a translation of the fourth German edition but is rather a fully revised fifth edition. For an author, it is impossible to translate his book without substantial rewriting and refining. All chapters have been more or less revised, and results which have been published since the last edition have been integrated. Many figures have been redrawn, while some are new; some altogether new chapters have also been included.

Last but not least, I wish to express again my sincere gratitude to all of my colleagues and friends, throughout the world, who helped me with all previous editions and especially with this English edition. Thanks are also extended to the staff of Springer-Verlag for encouraging me to write this English version and for correcting my imperfect English.

Berlin
July 2000

Roland Glaser

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About the Author

Roland Glaser Born in Jena, Germany in 1935. Studied biology at the Friedrich Schiller University, Jena, Ph.D. in 1961, qualified as a lecturer in 1965. From 1958 to 1961, scientist at the Atomic Energy Agency in Berlin (research: aquatic radioecology), and from 1962 to 1965 scientist at the Institute of Cardiology, Academy of Science in Berlin (with a focus on ion transport). From 1965 to 1970 assistant professor in Jena, from 1970 to 2000 full professor of biophysics at the Humboldt University, Berlin (research: biophysics of cell surfaces, shape and ionic states of erythrocytes, electro-manipulation of cells). In 1977 vice-president and from 1981 to 1985 president of the Society of Physical and Mathematical Biology of the GDR, from 1990 to 1992 dean of the Faculty of Science at the Humboldt University.

Roland Glaser was a member of the UNESCO European expert committee on biophysics (1976–1988), since 1978 a member of various commissions of the council of IUPAB, council member of EBEA (1993–1996) and of the national commission on radiation protection at the German Federal Ministry of Environmental Protection (1992–1998 and 2008–2010). He has also worked as an emeritus adviser for various organizations in the field of electromagnetic safety.

This book is the result of over 35 years of teaching. Following the first German edition in 1971, the textbook was continuously revised and updated in line with his experience from teaching as well as innumerable discussions with students and colleagues. The fourth German edition was published in 1996, and a fifth revised version was then published as the first English edition in 2001.

With this revised second English edition, the author reflects the enormous strides made in biophysics, especially in the fields of molecular and theoretical biophysics. While the book remains a basic textbook and provides the introductory background needed for fundamental training in biophysics, it also offers new insights into recent advances in biophysical knowledge.

List of Fundamental Constants and Symbols

The numbers in parentheses indicate equations in the text, where the symbols are explained or defined.

$\equiv$	identical
$=$	equal
$\stackrel{!}{=}$	equal by definition
$\approx$	approximately equal
~	proportional
A	Arrhenius-coefficient (Eq. 2.17)
A	affinity (Eq. 3.75)
A	area
a	chemical activity (Eq. 3.34)
B	magnetic flux density (Eq. 4.17)
b	electrophoretic mobility (Eq. 2.84)
C	electric capacity (Eq. 3.204)
C^*	complex electric capacitance (Eq. 3.211)
C_l	clearance-constant (Eq. 5.29)
C	heat capacity (Eq. 2.65)
c	molar concentration
c_0	speed of light in vacuum $= 2.998 \cdot 10^8$ m s^{-1}
D	diffusion coefficient (Eq. 3.131)
E	energy (general expression)
E	electric field strength (Eq. 2.44)
e	basis of natural logarithm = 2.71828
e	absolute amount of charge on electron $= 1.60218 \cdot 10^{-19}$ C
F	mechanical force
F	Faraday $= 9.6485 \cdot 10^4$ C val^{-1}
F	Helmholtz free energy (Eq. 3.22)
f	symbol for an arbitrary function
f	generalized coefficient of friction (Eq. 3.52)

f	activity coefficient (Eq. 3.34)
G	Gibbs free energy (Eq. 3.23)
G	electrical conductivity (Eq. 3.189)
g	specific conductivity (Eq. 3.209)
g	osmotic coefficient (Eq. 3.102)
H	enthalpy (Eq. 3.21)
$\mathbf{H}$	magnetic field strength (Eq. 4.17)
h	Planck's constant = $6.626 \cdot 10^{-34}$ J s = $4.136 \cdot 10^{-15}$ eV s
I	sound intensity (Eq. 4.12)
I	information (Eq. 2.6)
I	ionic strength (Eq. 2.56)
I_A	second moment of area (Eq. 3.232)
I_P	polar second moment of area (Eq. 3.233)
$\mathbf{i}$	unit vector in x-direction
j	imaginary unit = $\sqrt{-1}$
$\mathbf{j}$	unit vector in y-direction
j	electric current density (Eq. 4.23)
$\mathbf{J}$	flux (Eq. 3.125)
J	unidirectional flux in kinetic equations
K_p	equilibrium constant of isobaric chemical reactions (Eq. 3.71)
K	bending ($K = 1/R$), (Sect. 3.6.4)
k	Boltzmann's constant = $1.380658 \cdot 10^{-23}$ J K^{-1} = $8.6174 \cdot 10^{-5}$ eV K^{-1}
k	rate constant
L_i	phenomenological coefficient relating a flow to a force (Eq. 3.49)
L	decibel intensity of sound (Eq. 4.13)
l	distance, length
M	moment of force (Eq. 3.231)
m	mass
N	Avogadro's number = $6.0221367 \cdot 10^{23}$ mol^{-1}
n	number of particles, individuals etc.
P	mathematical probability (Sect. 2.1.2)
P	permeability coefficient (Eq. 3.133)
P	electrical power density (Eq. 4.23)
p	pressure
Q	heat
q	electric charge
R	molar gas constant = 8.314472 JK^{-1} mol^{-1}
R	radius of curvature ($R = 1/K$), (Eq. 3.227)
R	resistance coefficient relating a flow to a force (Eq. 3.50)
R	Ohm's resistance (reactance), (Sect. 3.5.13)
Re	Reynold's number (Eq. 3.234)
r	radius, radial distance
r	Donnan ratio (Eq. 3.123)
S	entropy (Eqs. 2.4 and 3.10)

T temperature
t time
U internal energy (Eq. 3.9)
V volume
$\bar{V}$ partial molar volume (Eq. 3.8)
$\mathbf{v}$ velocity
W thermodynamic probability (Eq. 2.5)
W work (Eq. 3.9)
$\mathbf{X}$ generalized force (Eq. 3.42)
x coordinate in an orthogonal system
x mole fraction (Eq. 3.35)
Y Young's modulus (Eq. 3.226)
Y^* electric admittance (Eq. 3.201)
y coordinate in an orthogonal system
z coordinate in an orthogonal system
z_i number of charges

α electrical polarizability (Eq. 2.48)
β_T isothermic compressibility (Eq. 2.66)
γ velocity gradient or shear rate (Eq. 3.220)
γ surface tension (Sect. 2.3.1)
δ difference of length
Δ sign, indicating a difference between two values
ε mechanical strain (Eq. 3.225)
ε dielectric constant or permeability number (Eq. 2.41)
ε_0 dielectric permittivity of vacuum $= 8.854187817 \cdot 10^{-12}$ C V^{-1} m^{-1}
ζ electrokinetic potential (Eq. 2.85)
η viscosity (Eq. 3.221)
κ Debye–Hückel constant (Eq. 2.55)
λ thermal conductivity (Eq. 4.1)
λ wavelength
μ magnetic permeability (Eq. 4.17)
μ_0 magnetic permeability of vacuum $= 1.2566370 \cdot 10^{-6}$ V s A^{-1} m^{-1} (Eq. 4.17)
μ electric dipole moment (Eq. 2.47)
μ_i chemical potential of the component i (Eq. 3.33)
$\tilde{\mu}_i$ electrochemical potential of the salt i (Eq. 3.41)
ν stoichiometric number (Eq. 3.1.65)
ν kinematic viscosity ($\nu = \eta/\rho$)
ν frequency in Hz ($\nu = \omega/2\pi$)
ξ degree of advancement of a chemical reaction (Eq. 3.73)
π osmotic pressure (Eq. 3.30)
ρ density
ρ charge density in space (Eq. 2.52)
σ Stefan–Boltzmann constant (Eq. 4.3)
σ mechanical stress (Eq. 3.224)

σ	entropy production (Eq. 3.63)
σ_0	surface charge density (Eq. 2.86)
σ	Staverman's reflection coefficient (Eq. 3.108)
τ	time constant
τ	sheer stress (Eq. 3.222)
$\mathbf{\Phi}$	Rayleigh's dissipation function (Eq. 3.64)
φ	fluidity ($\varphi = 1/\eta$) (Sect. 3.6.1)
χ	magnetic susceptibility (Eq. 4.18)
ψ	electrical potential (Eq. 2.43)
ω	angular frequency ($\omega = 2\ \pi v$)
ω	mobility factor (Eq. 3.52)