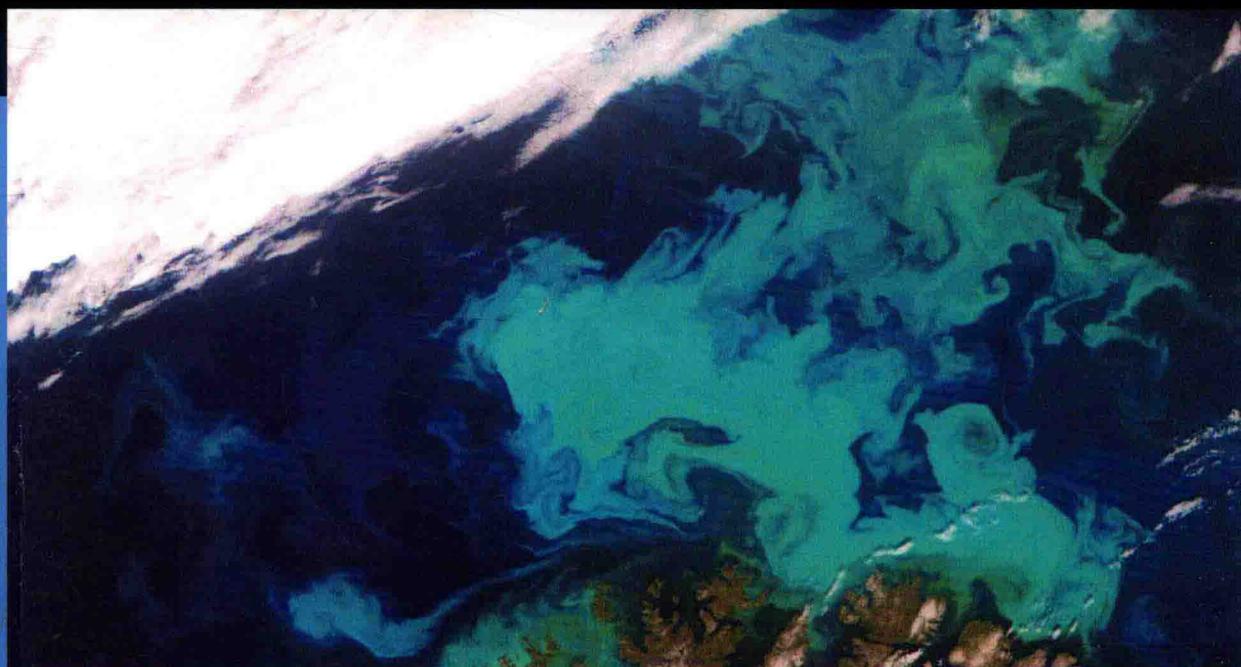


CHINESE MAINLAND EDITION

J. Claycomb, Jonathan Quoc P. Tran

Introductory Biophysics
Perspectives on the Living State

生物物理学导论



INTRODUCTORY BIOPHYSICS

PERSPECTIVES ON THE LIVING STATE

JAMES CLAYCOMB, PHD

Houston Baptist University

JONATHAN QUOC P. TRAN

University of Texas

Southwestern Medical Center



JONES AND BARTLETT PUBLISHERS

Sudbury, Massachusetts

BOSTON TORONTO LONDON SINGAPORE

NOT FOR SALE OUTSIDE OF THE CHINESE MAINLAND
Export or sale of this book outside the Chinese mainland is illegal

图书在版编目 (CIP) 数据

生物物理学导论 = Introductory Biophysics: Perspectives on the Living State: 英文 / (美) J. 克莱科姆 (J. Claycomb), J. Q. P. 特兰 (Jonathan Quoc P. Tran) 著. —影印本. —北京: 世界图书出版有限公司北京分公司, 2018.12

ISBN 978-7-5192-4860-4

I. ①生… II. ①J… ②J… III. ①生物物理学—教材—英文 IV. ①Q6

中国版本图书馆 CIP 数据核字 (2018) 第 173924 号

中文书名 生物物理学导论
英文书名 Introductory Biophysics: Perspectives on the Living State
著 者 J. Claycomb, Jonathan Quoc P. Tran
责任编辑 刘 慧 高 蓉
装帧设计 刘敬利

出版发行 世界图书出版有限公司北京分公司
地 址 北京市东城区朝内大街 137 号
邮 编 100010
电 话 010-64038355 (发行) 64033507 (总编室)
网 址 <http://www.wpcbj.com.cn>
邮 箱 wpcbjst@vip.163.com
销 售 新华书店
印 刷 北京建宏印刷有限公司
开 本 787 mm × 1092 mm 1/16
印 张 23.5
字 数 436 千字
版 次 2019 年 1 月第 1 版
印 次 2019 年 1 月第 1 次印刷
版权登记 01-2018-5239
国际书号 ISBN 978-7-5192-4860-4
定 价 99.00 元

版权所有 翻印必究

(如发现印装质量问题, 请与所购图书销售部门联系调换)

World Headquarters

Jones and Bartlett Publishers
40 Tall Pine Drive
Sudbury, MA 01776
978-443-5000
info@jbpub.com
www.jbpub.com

Jones and Bartlett Publishers
Canada
6339 Ormindale Way
Mississauga, Ontario L5V 1J2
Canada

Jones and Bartlett Publishers
International
Barb House, Barb Mews
London W6 7PA
United Kingdom

Jones and Bartlett's books and products are available through most bookstores and online book-sellers. To contact Jones and Bartlett Publishers directly, call 800-832-0034, fax 978-443-8000, or visit our website www.jbpub.com.

Substantial discounts on bulk quantities of Jones and Bartlett's publications are available to corporations, professional associations, and other qualified organizations. For details and specific discount information, contact the special sales department at Jones and Bartlett via the above contact information or send an email to specialsales@jbpub.com.

Copyright © 2011 by Jones and Bartlett Publishers, LLC

All rights reserved. No part of the material protected by this copyright may be reproduced or utilized in any form, electronic or mechanical, including photocopying, recording, or by any information storage and retrieval system, without written permission from the copyright owner.

QuickField™ is a trademark of Tera Analysis, Ltd. Copyright © 2009, Tera Analysis.

MATLAB® is a registered trademark of The MathWorks, Inc. Copyright © 2010, The MathWorks, Inc.

Production Credits

Publisher: David Pallai

Editorial Assistant: Molly Whitman

Production Manager: Tracey Chapman

Production Assistant: Ashlee Hazeltine

Associate Marketing Manager: Lindsay Ruggiero

V.P., Manufacturing and Inventory Control: Therese Connell

Composition: Lapiz Online

Cover Design: Scott Moden

Cover Image: Courtesy of Jacques Descloîtres, MODIS Rapid Response Team, NASA/GSFC

Printing and Binding: Malloy, Inc.

Cover Printing: Malloy, Inc.

Library of Congress Cataloging-in-Publication Data

Claycomb, James R.

Introductory biophysics: perspectives on the living state / James R. Claycomb, Jonathan Quoc P. Tran.
p. cm.

ISBN-13: 978-0-7637-7998-6 (hardcover)

ISBN-10: 0-7637-7998-9 (ibid.)

1. Biophysics. I. Tran, Jonathan Quoc P. II. Title.

QH505.C53 2011

571.4—dc22

ORIGINAL ENGLISH LANGUAGE EDITION PUBLISHED BY

Jones & Bartlett Learning, LLC

5 Wall Street

Burlington, MA 01803 USA

jblearning.com

Phone: 800-832-0034

Introductory Biophysics: Perspectives on the Living State, J. R. Claycomb © Copyright 2010 JONES & BARTLETT LEARNING, LLC. ALL RIGHT RESERVED

NOT FOR SALE OUTSIDE OF THE CHINESE MAINLAND.

Export or sale of this book outside the Chinese mainland is illegal.

*Dedicated to the memory of
John Vay*

Introduction

Physics is the most basic natural science. It is the lowest-level science on a tree diagram representing the natural sciences. Other sciences such as chemistry and biology are higher-level sciences. Now it is possible to begin on one of the natural science branches and proceed quite a distance without knowledge of the more basic physical principles such as Newton's laws and gravitation. General physics, for example, is rarely a prerequisite for introductory biology and chemistry. To sprout new branches in our understanding of nature, and biology in particular, the tools of basic physics and chemistry are often required.

One goal of this textbook is to introduce biophysical theory concurrently with computer simulation. Another goal is to emphasize several important themes such as the role of entropy and the ubiquity of the statistical Boltzmann factor describing many aspects of the living state from the establishment of membrane potentials to the sedimentation of cell cultures. A key perspective of the textbook considers life in relation to the universe as a whole.

Additional computer simulation examples and exercises in the text and on the companion CD enable modeling of biophysical phenomena such as diffusion, establishment of membrane potential, bioimpedance, and the electrical response of cells and organelles to external fields. Dynamical models include the propagation of action potentials, nonlinear oscillations in population dynamics, and DNA vibrational modes. The formation of fractal structures, branching networks, and patterns in biology are also simulated. Contact with simulation methods further reinforces biophysical theory and strengthens the connection between physics and the life sciences.

Topics are arranged in increasing size scale and complexity. Chapters 1 and 2 give an introductory overview of biological structure and molecular forces. Chapters 3 through 6 cover heat transfer, thermodynamics, statistical mechanics, and diffusion, which play important roles in the biological domain. Chapter 7 covers fluid dynamics and the motion of bodies in fluid media. Bioenergetics, molecular motors, and the light absorption of biomolecules are discussed in Chapter 8. Chapters 9 through 11 discuss electrical and mechanical aspects of biophysics, including the passive response of cells and tissue to electric fields, field-induced stresses in biomaterials, and the propagation of action potentials in nerve cells. Biomagnetism and magnetic

measurements are discussed in Chapter 12. Nonlinearity, chaos, and complexity in the life sciences are covered in Chapters 13 and 14. The textbook concludes with an introduction to astrobiology in Chapter 15.

Acknowledgments

We would like to acknowledge Vladimir Podnos for helpful suggestions for implementing QuickField™ for biophysical applications, software support from The MathWorks, Inc. and Tera Analysis. Thanks to Barbara Benitez-Gucciardi for sharing insights in computational biology and the F–N model. We are thankful for many helpful conversations with Saul Trevino and Gardo Blado on protein folding and statistical physics, respectively. Many thanks are due John H. Miller, Jr. for introducing us to many topics covered here from biomagnetism to torque generation in ATP synthase. We are grateful for helpful suggestions from Audrius Brazdeikis and for supplying fetal magnetocardiography data using SQUIDS. Thanks to Cindy Troung and Anum Umer for their investigations on the effects of microgravity on the human body. We are grateful for figure support from NASA and ADInstruments. J. R. C. acknowledges support of the Texas Center for Superconductivity at the University of Houston.

Table of Contents

Introduction v

Chapter 1 Building Blocks and Structure 1

- 1.1 Atoms and Ions 1
 - 1.1.1 Subatomic Particles 1
 - 1.1.2 Atomic Constituents of Life 3
 - 1.1.3 Ions 3
- 1.2 Molecules Essential for Life 4
 - 1.2.1 Water 4
 - 1.2.2 Proteins 5
 - 1.2.3 Lipids 8
 - 1.2.4 Carbohydrates 10
 - 1.2.5 Cholesterol 10
 - 1.2.6 Nucleic Acid 11
- 1.3 What Is Life? 11
 - 1.3.1 Requirements for Life 12
 - 1.3.2 Domains of Life 12
 - 1.3.3 Characteristics of Living Cells 12
 - 1.3.4 Structure of Living Cells 13
 - 1.3.5 Boundary of Life 13

Chapter 2 Living State Interactions 17

- 2.1 Forces and Molecular Bonds 17
 - 2.1.1 Ionic Bonds 18
 - 2.1.2 Covalent Bonds 19
 - 2.1.3 Hydrogen Bonds 19
 - 2.1.4 Van der Waal Forces 20
- 2.2 Electric and Thermal Interactions 20
- 2.3 Electric Dipoles 21
 - 2.3.1 Polarization and Induced Dipoles 23

	2.4	Casimir Interactions	24
	2.5	Domains of Physics in Biology	26
		Exercises	27
Chapter 3		Heat Transfer in Biomaterials	29
	3.1	Heat Transfer Mechanisms	29
		3.1.1 Conduction	30
		3.1.2 Convection	30
		3.1.3 Radiation	31
	3.2	The Heat Equation	32
		3.2.1 Transient Heat Flow	32
		3.2.2 Steady State Heat Flow	34
	3.3	Joule Heating of Tissue	35
		Exercises	37
Chapter 4		Living State Thermodynamics	39
	4.1	Thermodynamic Equilibrium	40
	4.2	First Law of Thermodynamics and Conservation of Energy	40
	4.3	Entropy and the Second Law of Thermodynamics	41
		4.3.1 Does Life Violate the Second Law?	41
		4.3.2 Measures of Entropy?	42
		4.3.3 Free Expansion of a Gas	42
	4.4	Physics of Many Particle Systems	43
		4.4.1 How Boltzmann Factors in Biology	44
		4.4.2 Canonical Partition Function	45
		4.4.3 Average Energy	46
		4.4.4 Entropy and Free Energy	47
		4.4.5 Heat Capacity	48
	4.5	Two-State Systems	49
	4.6	Continuous Energy Distribution	50
	4.7	Composite Systems	50
		4.7.1 DNA Stretching	51
	4.8	Casimir Contribution to the Free Energy	53
		4.8.1 Lipid Bilayer Tubes	53
		4.8.2 Rouleaux	53
	4.9	Protein Folding and Unfolding	55
		4.9.1 Protein Unfolding	55
		4.9.2 Levinthal's Paradox	55
		4.9.3 Energy Landscape	56

- 4.9.4 Folding on a Lattice 57
- 4.9.5 Monte Carlo Methods 58
- 4.9.6 Folding@home 59

Exercises 59

Chapter 5 Open Systems and Chemical Thermodynamics 61

- 5.1 Enthalpy, Gibbs Free Energy, and Chemical Potential 61
- 5.2 Chemical Reactions 64
 - 5.2.1 First-Order Reactions 64
 - 5.2.2 Second-Order Reactions 65
- 5.3 Activation Energy and Rate Constants 66
 - 5.3.1 Detailed Balance 68
 - 5.3.2 Nitrogen Fixation 69
- 5.4 Enzymatic Reactions 70
- 5.5 ATP Hydrolysis and Synthesis 73
- 5.6 Entropy of Mixing 74
- 5.7 The Grand Canonical Ensemble 74
- 5.8 Hemoglobin 76

Exercises 77

Chapter 6 Diffusion and Transport 79

- 6.1 Maxwell–Boltzmann Statistics 79
- 6.2 Brownian Motion 81
- 6.3 Fick’s Laws of Diffusion 84
 - 6.3.1 Fick’s First Law 84
 - 6.3.2 Fick’s Second Law 85
 - 6.3.3 Quantum Diffusion 86
 - 6.3.4 Time-Independent Concentrations 86
 - 6.3.5 Fick’s Law for Growing Bacterial Cultures 87
- 6.4 Sedimentation of Cell Cultures 88
- 6.5 Diffusion in a Centrifuge 89
- 6.6 Diffusion in an Electric Field 91
- 6.7 Lateral Diffusion in Membranes 92
- 6.8 Navier–Stokes Equation 93
 - 6.8.1 Reynolds Number 94
- 6.9 Low Reynolds Number Transport 95
 - 6.9.1 Purcell’s “Life at Low Reynolds Number” 95
 - 6.9.2 Coasting Distance of a Bacterium 95
- 6.10 Active and Passive Membrane Transport 97

Exercises 98

Chapter 7	Fluids	101
7.1	Laminar and Turbulent Fluid Flow	101
7.2	Bernoulli's Equation	102
7.3	Equation of Continuity	103
7.4	Venturi Effect	104
7.5	Fluid Dynamics of Circulatory Systems	106
7.5.1	Viscous Flow	106
7.5.2	Vessel Constriction and Aneurysm	107
7.5.3	Variation of Blood Pressure with Depth	108
7.5.4	Microgravity Effects	108
7.6	Capillary Action	109
	Exercises	110
Chapter 8	Bioenergetics and Molecular Motors	111
8.1	Kinesins, Dyneins, and Microtubule Dynamics	111
8.2	Brownian Motors	113
8.2.1	Feynman Ratchet	113
8.2.2	Kinesin Brownian Dynamics	115
8.2.3	Myosin Brownian Dynamics	115
8.3	ATP Synthesis in Mitochondria	116
8.3.1	Electron Transport Chain	116
8.3.2	ATP Synthase	117
8.3.3	Torque Generation in ATP Synthase	118
8.4	Photosynthesis in Chloroplasts	118
8.4.1	Photosystem II	120
8.4.2	Photosystem I	120
8.5	Light Absorption in Biomolecules	120
8.6	Vibrational Spectra of Biomolecules	122
8.6.1	Square Well Potential	122
8.6.2	Harmonic Oscillator Potential	122
	Exercises	125
Chapter 9	Passive Electrical Properties of Living Cells	127
9.1	Poisson–Boltzmann Equation	127
9.1.1	One–One Valent Electrolytes	129
9.1.2	Low Field Limit	130
9.1.3	Spherical Solution	130
9.2	Intrinsic Membrane Potentials	131
9.3	Induced Membrane Potentials	132
9.3.1	Plasma Membrane	132

9.3.2	Liposome in a Static Electric Field	134
9.3.3	Spherical Cell in an Alternating Electric Field	135
9.3.4	Inertial Effects in Field-Induced Counterion Motion	136
9.3.5	Induced Potentials in Organelle Membranes	136
9.3.6	Mitochondrion in an Alternating Electric Field	137
9.4	Bioimpedance	138
9.4.1	Time Harmonic Current Flow	138
9.4.2	Dielectric Spectroscopy	139
9.4.3	Debye Relaxation Model	142
9.4.4	Cole Equation	142
9.4.5	Maxwell–Wagner Effect	143
9.4.6	Skin Impedance	144
9.4.7	Electrode Polarization	144
9.5	Bioimpedance Simulator	145
9.6	Nonlinear Effects	148
	Exercises	149

Chapter 10 Nerve Conduction 153

10.1	Nerve Impulses	153
10.2	Neurotransmitters and Synapses	154
10.3	Passive Transport in Dendrites	155
10.4	Active Transport and the Hodgkin–Huxley Equations	156
10.5	Simulation of Action Potential	160
10.5.1	Excitation Threshold	160
10.5.2	Neuronal Refractoriness	160
10.5.3	Repetitive Spiking	161
10.6	FitzHugh–Nagumo Model	163
10.7	Action Potentials in the Earthworm Nerve Fiber	166
	Exercises	168

Chapter 11 Mechanical Properties of Biomaterials 169

11.1	Elastic Moduli	169
11.1.1	Young’s Modulus	169
11.1.2	Shear Modulus	170
11.1.3	Poisson’s Ratio	171
11.2	Electric Stresses in Biological Membranes	172
11.3	Mechanical Effects of Microgravity During Spaceflight	172
	Exercises	173

Chapter 12 Biomagnetism 177

- 12.1 Biomagnetic Field Sources 177
 - 12.1.1 Current Dipole Model 179
 - 12.1.2 Vector Potential Formulation 180
- 12.2 Nerve Impulses 180
- 12.3 Magnetotactic Bacteria 181
- 12.4 SQUID Magnetometry 182
 - 12.4.1 Josephson Effect 184
 - 12.4.2 Flux-Locked Loop 186
 - 12.4.3 Intrinsic Noise Factors 187
 - 12.4.4 Extrinsic Noise Factors 187
 - 12.4.5 Digital Filters 189
- 12.5 Magnetocardiography 189
- 12.6 Fetal Magnetocardiography 190
- 12.7 Magnetoencephalography 191
- Exercises 193

Chapter 13 Nonlinearity and Chaos in Biological Systems 195

- 13.1 Chaotic Dynamics 195
 - 13.1.1 Characteristics of Chaotic Dynamics 196
 - 13.1.2 Sensitive Dependence on Initial Conditions 197
 - 13.1.3 Phase Space 197
 - 13.1.4 Phase Space Reconstruction 198
 - 13.1.5 Poincaré Sections 199
 - 13.1.6 Lyapunov Exponents 200
 - 13.1.7 Power Spectra 200
- 13.2 Population Growth in a Limited Environment 202
- 13.3 Predator–Prey Models of Population Dynamics 203
- 13.4 Discrete Logistic Equation 204
 - 13.4.1 Period-Doubling Route to Chaos 206
 - 13.4.2 Bifurcation Diagrams 210
 - 13.4.3 Lyapunov Exponent of the Logistic Equation 212
 - 13.4.4 Shannon Entropy 213
- 13.5 Chaos in the Heart 215
- 13.6 Reaction Diffusion Equations 216
 - 13.6.1 Action Potentials 216
 - 13.6.2 Fertilization Calcium Waves 216
 - 13.6.3 Pattern Formation 217
- 13.7 Dynamics of the Driven Hodgkin–Huxley System 217
- 13.8 Models of DNA Motility 218
- Exercises 221

Chapter 14	Fractals and Complexity in the Life Sciences	225
14.1	Fractal Geometry	225
14.1.1	Computing Fractal Dimension	228
14.2	Fractal Structures in Biology	231
14.2.1	Fractal Ferns	231
14.2.2	Diffusion-Limited Aggregation	233
14.3	Power Laws in Biology	233
14.4	Self-Organized Criticality	235
14.4.1	BTW Sandpile Model	236
14.5	Extinction in the Bak–Sneppen Model	238
14.6	Power Law Behavior in Chemical Reactions	239
14.7	The Game of Life	241
14.7.1	SOC in the Game of Life	244
	Exercises	245
Chapter 15	Life and the Universe	247
15.1	Astrobiology	247
15.2	Extremophiles	248
15.3	Primordial Soup, Interstellar Gas, and Dust	249
15.3.1	The Miller Experiment	249
15.3.2	Chemistry of the Interstellar Medium	250
15.4	Searches for Life in the Solar System	251
15.4.1	Mars	251
15.4.2	Europa	256
15.4.3	Lake Vostok	257
15.5	Search for Life Outside the Solar System	258
15.5.1	Extrasolar Planets	258
15.5.2	SETI Initiatives	258
15.5.3	Anticoded Signals	259
15.5.4	Frequency Domain Searches	259
15.5.5	Radio Interferometry	260
15.5.6	The Drake Equation	261
15.6	Implications for Life in the Multiverse Picture	263
15.6.1	The Multiverse	263
15.6.2	The Anthropic Principle	264
15.6.3	Multiverse Cosmological Models	265
	Exercises	269

Appendix 1: Mathematical Formulas	273
Appendix 2: Overview of MATLAB®	281
Appendix 3: Derivation of the Heat Equation	289
Appendix 4: Derivation of Shannon's Entropy Formula	291
Exercises	294
Appendix 5: Thermodynamic Identities	295
Appendix 6: Kramers–Kronig Transformations	297
Appendix 7: Solution to the One-Dimensional Schrödinger Equation	299
Exercises	302
Appendix 8: Biophysical Applications of QuickField™	303
Appendix 9: Biological Material Properties	309
Appendix 10: Solutions of the Linearized Poisson–Boltzmann Equation	313
Exercises	323
References and Further Reading	325
Index	339

1

Building Blocks and Structure

- 1.1 Atoms and Ions
 - 1.1.1 Subatomic Particles
 - 1.1.2 Atomic Constituents of Life
 - 1.1.3 Ions
- 1.2 Molecules Essential for Life
 - 1.2.1 Water
 - 1.2.2 Proteins
 - 1.2.3 Lipids
 - 1.2.4 Carbohydrates
 - 1.2.5 Cholesterol
 - 1.2.6 Nucleic Acids
- 1.3 What Is Life?
 - 1.3.1 Requirements for Life
 - 1.3.2 Domains of Life
 - 1.3.3 Characteristics of Living Cells
 - 1.3.4 Structure of Living Cells
 - 1.3.5 Boundary of Life

■ 1.1 Atoms and Ions

1.1.1 Subatomic Particles

All matter essential to life is made up of atoms consisting of protons, neutrons, and electrons. The electron is a stable particle belonging to a class of subatomic particles known as fermions. The electron is elementary and without internal structure. Table 1.1 gives a list of elementary particles according to the standard model of particle physics. Protons and neutrons are composite particles made out of combinations of three up (u) and down (d) quarks. The proton is (uud) while the neutron is (udd). The four other quarks: strange (s), charm (c), top (t), and bottom (b) do not form stable particles and therefore do not participate in the physics of the living state.

Another particle essential to life is the photon (γ) that is a massless member of the Boson class of particles. Without the photon, energy could not travel from the Sun to

Table 1.1 Particles of the Standard Model

Fermions			Bosons
u	c	t	γ
d	s	b	Z
ν_e	ν_μ	ν_τ	W
e^-	μ	τ	g

the Earth and warm our planet. Plants absorb photons to produce adenosine triphosphate (ATP) and to fix carbon that is consumed by more complex organisms on the food chain such as humans.

In Paul Dirac's theory of relativistic quantum mechanics, antiparticles were predicted that were later discovered in cloud chamber experiments. It turns out that for every particle species in nature there is a corresponding antiparticle, although antimatter is quite scarce, at least on Earth. Antimatter plays a key role in the strong nuclear force through the exchange of π mesons. These mesons are quark-antiquark pairs exchanged between nucleons binding the nucleus together. Antimatter is therefore essential for the existence of stable atoms and hence, life. Antimatter is also employed in medical imaging using positron emission tomography (PET) where the positron e^+ is the positively charged antiparticle of the electron. Gamma rays are detected in PET scans that are produced by the annihilation of matter and antimatter according to the reaction $e^+ + e^- \rightarrow 2\gamma$. From Einstein's mass energy relation and the energy of each photon $E = hf$ with $f\lambda = c$, the wavelength of the gamma rays emitted in PET are $\lambda = h/m_e c = 2.43 \text{ pm}$.

The neutrino (ν), or "little neutral one," predicted by Wolfgang Pauli, is a participant of beta decay and other nuclear reactions. Roughly 10^{12} solar neutrinos pass through our bodies each second. Neutrinos are weakly interacting, so this rate does not change during the night as neutrinos pass straight through the Earth, only very occasionally interacting with matter. Without neutrinos, nuclear reactions essential to stars would not take place. The little neutral one is therefore essential for life in this regard.

The gluon (g) is a key participant in the strong nuclear force binding quarks in nucleons and mesons. Other particles of the standard model may not contribute directly to the physics of the living state but may be a natural consequence of a universe capable of sustaining life.

Highly energetic subatomic particles in cosmic rays can also influence life processes by breaking molecular bonds and causing genetic mutations. Fortunately, the Earth's atmosphere serves to greatly attenuate the flux of cosmic rays. The ozone layer is especially important in absorbing harmful solar ultraviolet radiation. Astronauts in space habitats are more vulnerable to solar protons that can cause health problems if received in excessive doses. Solar flares and coronal mass ejections can generate lethal