#### THE EMERGENCE OF LIFE

The origin of life from inert chemical compounds has been the focus of much research for decades, both experimentally and philosophically. Connecting both approaches, Luisi takes the reader through the transition to life, from prebiotic chemistry to synthetic biology. This book presents a systematic course discussing the successive stages of self-organization, emergence, self-replication, autopoiesis, synthetic compartments and construction of cellular models, in order to demonstrate the spontaneous increase in complexity from inanimate matter to the first cellular life forms. A chapter is dedicated to each of these steps, using a number of synthetic and biological examples. The theory of autopoiesis leads into the idea of compartments, which is discussed with an emphasis on vesicles and other orderly aggregates. The final chapter uses liposomes and vesicles to explain the synthetic biology of cellular systems, as well as describing attempts to generate minimal cellular life within the laboratory. With challenging review questions at the end of each chapter, this book will appeal to graduate students and academics researching the origin of life and related areas such as biochemistry, molecular biology, biophysics, and natural sciences. Additional resources for this title are available online at www.cambridge.org/9780521821179.

PIER LUIGI LUISI became Professor Emeritus (Macromolecular Chemistry) at ETH-Zürich in 1982, where he also acted as Dean of the Chemistry Department; he is currently a professor of Biochemistry at the University of Rome 3. He has authored *c*. 300 papers in the fields of enzymology, molecular biology, peptide chemistry, self-organization and self-reproduction of chemical systems, and models for cells.

Cambridge University Press 0521821177 - The Emergence of Life: From Chemical Origins to Synthetic Biology Pier Luigi Luisi Frontmatter <u>More information</u>

## THE EMERGENCE OF LIFE

From Chemical Origins to Synthetic Biology

PIER LUIGI LUISI University of Rome 3



CAMBRIDGE UNIVERSITY PRESS Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo

> Cambridge University Press The Edinburgh Building, Cambridge CB2 2RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org Information on this title: www.cambridge.org/9780521821179

© P. L. Luisi 2006

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 2006

Printed in the United Kingdom at the University Press, Cambridge

A catalog record for this publication is available from the British Library

ISBN-13 978-0-521-82117-9 hardback ISBN-10 0-521-82117-7 hardback

Cambridge University Press has no responsibility for the persistence or accuracy of URLs for external or third-party internet websites referred to in this publication, and does not guarantee that any content on such websites is, or will remain, accurate or appropriate.

Cambridge University Press 0521821177 - The Emergence of Life: From Chemical Origins to Synthetic Biology Pier Luigi Luisi Frontmatter More information

To my wife Claudia

### Contents

	Preface	page xi
	Acknowledgments	xiii
	List of books on the origin of life	xiv
1	Conceptual framework of research on the origin of life on Earth	1
	Introduction	1
	Determinism and contingency in the origin of life	4
	Only one start – or many?	10
	The anthropic principle, SETI, and the creationists	12
	Questions for the reader	16
2	Approaches to the definitions of life	17
	Introduction	17
	A historical framework	19
	The visit of the Green Man	23
	Main operational approaches to the origin of life	26
	I. The "prebiotic" RNA world	27
	II. The compartmentalistic approach	29
	III. The "prebiotic metabolism" approach	31
	Concluding remarks	36
	Questions for the reader	37
3	Selection in prebiotic chemistry: why this and not that?	38
	Introduction	38
	From Oparin to Miller – and beyond	40
	Other sources of organic molecules	46
	Miller's $\alpha$ -amino acids: why do they form?	50
	Some notes on homochirality	52
	Concluding remarks	56
	Questions for the reader	58

vii	i <i>Contents</i>	
4	The bottle neck: macromolecular sequences	59
	Introduction	59
	Proteins and nucleic acids are copolymers	60
	The quest for macromolecular sequences	62
	What about polynucleotides?	65
	A grain of sand in the Sahara	68
	The "never-born proteins"	70
	A model for the aetiology of macromolecular sequences – and a	
	testable one	72
	Homochirality in chains	76
	Chain chirality and chain growth	78
	Concluding remarks	82
	Questions for the reader	84
5	Self-organization	85
	Introduction	85
	Self-organization of simpler molecular systems	87
	Self-organization and autocatalysis	91
	Polymerization	93
	Self-organization and kinetic control	95
	Self-organization and breaking of symmetry	97
	Complex biological systems	100
	Self-organization and finality	105
	Out-of-equilibrium self-organization	106
	Concluding remarks	109
	Questions for the reader	111
6	The notion of emergence	112
	Introduction	112
	A few simple examples	114
	Emergence and reductionism	116
	Deducibility and predictability	117
	Downward causation	119
	Emergence and non-linearity	120
	Life as an emergent property	123
	Concluding remarks	125
	Questions for the reader	128
7	Self-replication and self-reproduction	129
	Introduction	129
	Self-replication and non-linearity	129
	Myths and realities of self-replication	132
	Self-replicating, enzyme-free chemical systems	133

#### CAMBRIDGE

Cambridge University Press 0521821177 - The Emergence of Life: From Chemical Origins to Synthetic Biology Pier Luigi Luisi Frontmatter More information

	Contents	ix
	One more step towards complexity	141
	Self-reproducing micelles and vesicles	143
	Concluding remarks	153
	Questions for the reader	154
8	Autopoiesis: the logic of cellular life	155
	Introduction	155
	Historical background	156
	Basic autopoiesis	157
	Criteria of autopoiesis	159
	What autopoiesis does not include	160
	Chemical autopoiesis	162
	Autopoiesis and cognition	164
	Cognition and enaction	167
	Necessary and sufficient?	169
	One glance further up: from autopoiesis to the cognitive domain	172
	Social autopoiesis	175
	Autopoiesis and the chemoton: a comparison of the views of Ganti	
	with those of Maturana and Varela	177
	Concluding remarks	179
	Questions for the reader	181
9	Compartments	182
	Introduction	182
	Surfactant aggregates	182
	Aqueous micelles	187
	Compartmentation in reverse micelles	189
	Cubic phases	198
	Size and structural properties of vesicles	199
	The water pool and the membrane of vesicles	203
	Prebiotic membranes	206
	The case of oleate vesicles	209
	Concluding remarks	211
	Questions for the reader	213
10	Reactivity and transformation of vesicles	214
	Introduction	214
	Simple reactions in liposomes	214
	Giant vesicles	222
	Self-reproduction of vesicles	223
	The matrix effect	233
	The importance of size for the competition of vesicles	237

х

1

	Contents	
	Concluding remarks	240
	Questions for the reader	242
1	Approaches to the minimal cell	243
	Introduction	243
	The notion of the minimal cell	244
	The minimal RNA cell	246
	The minimal genome	247
	Further speculations on the minimal genome	251
	The road map to the minimal cell. 1: Complex biochemical	
	reactions in vesicles	254
	The road map to the minimal cell. 2: Protein expression in vesicles	259
	The road map to the minimal cell. What comes next?	263
	Concluding remarks	265
	Questions for the reader	267
	Outlook	268
	References	271
	Index	301

#### Preface

There are already so many books on the origin of life, as listed on pages xiv–xi. Why then write another?

There are two answers to this question. The first comes from the desire to write a book for students – rather than a specialist book – in which the various phases of the transition to life would be laid out in a discursive way that illustrates the basic principles of self-organization, emergence, self-reproduction, autocatalysis, and their mutual interactions. Another important aspect of this teaching aim is to take into consideration the philosophical implications that are present, more or less consciously, in the field of the origin of life. I believe in fact that the younger generation of chemists and molecular biologists should be more cognizant of the connections between the biological and the philosophical quest, so as possibly to integrate the most basic language of epistemology, and see their science work in a broader dimension. This integration, when taken seriously, may also foster an interaction with the ethical and humanistic aspects of life. The age-old question: "what can science say about the domains of psyche, ethics, or consciousness?" is usually discarded by most scientists with a wave of the hand. This behavior is one of the main reasons why science has lost contact with the broad public - and again, it would be desirable that the younger generations take a different stand. Although this is not a central issue of this book, I hope to offer some hints on how this new approach might be defined.

While all these reasons are centered on the target of teaching, the other reason for the coming to being of this book is more subtle. It comes from the perception of a shift in the field of the origin of life, a new "Zeitgeist" (spirit of time), which makes it timely to propose a new discourse.

One aspect of the new Zeitgeist is the influence of system biology, a new operational framework where the behavior of an entire complex biological system is more important than – or as important as – the individual molecular events. Although the origin of this novel biology lies in the development of analytical tools, more than in Cambridge University Press 0521821177 - The Emergence of Life: From Chemical Origins to Synthetic Biology Pier Luigi Luisi Frontmatter More information

xii

#### Preface

a basic philosophical shift, the final consequence is an operational framework which is at some distance from the reductionistic approach of viewing life as a reaction based solely on nucleic acids. I believe that the exaggerated emphasis given until now to the prebiotic RNA world probably needs to be brought back into balance. And I believe the balance must be based on a more integrative view of cellular processes, even at the stage of the origin of life. Thus, I will give here proper emphasis to the autopoietic view of minimal life – which is generally not considered in other books. The latter chapters are devoted to the chemical and physical properties of compartments, vesicles in particular, and these are more technical in nature. In fact, this book suffers from that kind of heterogeneity that characterizes the field of the origin of life: on the one hand it thrives on epistemological concepts; and on the other hand it is based on experimental organic and physical chemistry. This double nature, far from being a problem, constitutes the very complexity and beauty of the field.

More generally, I will try to illustrate the different views on the origin of life and early evolution – notions like determinism and contingency will come into focus. All these scientific views are based on the postulate that life on Earth comes from inanimate matter; and a corollary of this postulate is that it might be possible to reconstitute life in the laboratory, at least in some elementary form. The ambition of understanding the prebiotic chemistry leading to the transition to life, and ultimately, to the Faustian dream of making life on the workbench, underlies the whole field – and is also the common thread of this book.

I do not know whether this dream will be fulfilled, but in closing I would like to cite Friedrich Rolle, a German philosopher and biologist, who, in 1863, writing about the hypothesis that life arose from inanimate matter, stated:

# The general reasons for this assumption are really so impelling, that no doubt sooner or later it will be possible to show this in a clear and broadly scientific way, or even to repeat the process by experimentation.

This was written one and a half centuries ago and yet today we do not know whether we will ever get there. This book makes no pretence of showing the way, but as the pages unfold we will see some of the reasons why this enterprise is so difficult; and this in itself is a kind of positive knowledge.

## Acknowledgments

A number of colleagues were very kind and helpful with their advice. I would like to thank Antonio Lazcano, and Albert Eschenmoser, who in different ways helped me with their frank comments; and Meir Lahav, Joseph Ribo, Jeffrey Bada, and David Deamer. Particular thanks are due to Dr. Pasquale Stano, whose help has been essential, particularly, but not only, with the bibliography; also Rachel Fajella helped with the editing of some parts of the manuscript. I am also particularly indebted to Angelo Merante for the illustrations and the formatting of the manuscript: without him, the manuscript would still be in my drawers. Last, but not least, I want to thank my students of the University of Rome 3, their positive feedback at the very early stages of the manuscript was very important.

xiii

#### Books on the origin of life

- Bastian, H. (1872). The Beginnings of Life. Appleton.
- Pryer, W. T. (1880). Die Hypothesen über den Ursprung des Lebens. Berlin.
- Leduc, S. (1907). Les Bases Physiques de la Vie. Masson.
- Osborn, H. (1918). The Origin and Evolution of Life. Charles Schribner and Sons.
- Oparin, A. (1924). *Proishkhozhddenie Zhisni*. Moskowski Rabocii. (In Russian, translated into English as: Oparin, A., 1938. *The Origin of Life*. MacMillan).
- Haldane, J. B. S. (1929), The origin of life. In *The Origin of Life*, ed. J. D. Bernal. World Publishing Co.
- Bernal, J. D. (1951). *The Physical Basis of Life*. Routledge and Paul.
- Oparin, A. (1953). The Origin of Life. Dover Publications.
- Haldane, J. B. S. (1954). The origin of life. New Biol., 16, 12.
- Schrödinger, E. (1956). What is Life? And other Scientific Essays. Cambridge University Press.
- Oparin, A. (1957). The Origin of Life on Earth, 3rd edn. Academic Press.
- Crick, F. (1966). Of Molecules and Men. University of Washington Press.
- Bernal, J. D. (1967). The Origin of Life. World Publishing Co.
- (1971). Ursprung des Lebens. Editions Rencontre.
- Fox, S. W. and Dose, K. (1972). Molecular Evolution and the Origin of Life. Freeman.
- Orgel, L. E. (1973). The Origins of Life. Wiley.
- Miller, S. L. and Orgel, L. E. (1974). The Origin of Life on Earth. Prentice Hall.
- Ponnamperuma, C. (1981). Comets and the Origin of Life. Reidel.
- Cairns-Smith, A. G. (1982). *Genetic Takeover and the Mineral Origin of Life*. Cambridge University Press.
- Day, W. (1984). *Genesis on Planet Earth: the Search for Life's Beginnings*. Yale University Press.
- Cairns-Smith, A. G. (1985). *Seven Clues to the Origin of Life*. Cambridge University Press.
- Shapiro, R. (1986). Origins: A Skeptic's Guide to the Creation of Life on Earth. Summit.
- Fox, S. W. (1988). The Emergence of Life. Basic Books.
- De Duve, C. (1991). *Blueprint for a Cell: The Nature and the Origin of Life*. Portland Press.
- Eigen, M. and Winkler-Oswatitisch, R. (1992). *Steps Towards Life*. Oxford University Press.

Morowitz, H. J. (1992). Beginning of Cellular Life. Yale University Press.

Margulis, L. and Sagan, D. (1995). What is Life? Weidenfeld and Nicholson.

Books on the origin of life

XV

Rizzotti, M., ed. (1996). Defining Life. University of Padua.

- Thomas, P. J., Chyba, C. F., and McKay, C P., eds. (1997). *Comets and the Origins and Evolution of Life*. Springer Verlag.
- Brack, A., ed. (1998). The Molecular Origin of Life. Cambridge University Press.
- Dyson, F. (1999). Origins of Life, 2nd ed. Cambridge University Press.
- Fry, I. (1999). The Emergence of Life on Earth. Free Association Books.
- Maynard Smith, J. and Szathmáry, E. (1999). The Origins of Life. Oxford University Press.
- Varela, F. J. (2000). El Fenomeno de la Vida. Dolmen Ensayo.
- Willis, C. and Bada, J. (2000). The Spark of Life. Perseus Publications.
- Zubay, G. (2000). Origins of Life on the Earth and in the Cosmos. Academic Press.
- Schwabe, C. (2001). The Genomic Potential Hypothesis, a Chemist's View of the Origins, Evolution and Unfolding of Life. Landes Bioscience.
- Day, W. (2002). *How Life Began: the Genesis of Life on Earth*. Foundation for New Directions.
- De Duve, C. (2002). *Life Evolving, Molecules, Mind and Meaning*. Oxford University Press.
- Schopf, J. W., ed. (2002). *Life's Origin, The Beginning of Biological Evolution*. California University Press.
- Ganti, T. (2003). The Principles of Life. Oxford University Press.
- Popa, R. (2004). *Between Necessity and Probability: Searching for the Definition and Origin of Life*. Springer Verlag.
- Ribas de Pouplan L., ed. (2004). The Genetic Code and the Origin of Life. Kluwer.
- Luisi, P. L. (2006). *The Emergence of Life: From Chemical Origins to Synthetic Biology*. Cambridge University Press.