The Virtual Laboratory

Springer-Verlag Berlin Heidelberg GmbH

Hans Meinhardt

The Algorithmic Beauty of Sea Shells

Third Edition

With Contributions and Images
by Przemyslaw Prusinkiewicz
and Deborah R. Fowler

With 120 Illustrations, 107 in Color,
and CD-ROM

Springer

Hans Meinhardt
Max-Planck-Institut for Developmental Biology
Spemannstr. 35
72076 Tübingen
Germany
hans.meinhardt@tuebingen.mpg.de

Series Editor
Przemyslaw Prusinkiewicz

Cataloging-in-Publication Data applied for
Bibliographic information published by Die Deutsche Bibliothek
Die Deutsche Bibliothek lists this publication in the Deutsche Nationalbibliografie; detailed bibliographic data is available in the internet at: <http://dnb.ddb.de>.

Additional material to this book can be downloaded from http://extras.springer.com
ISBN 978-3-662-05293-8 ISBN 978-3-662-05291-4 (eBook)
DOI 10.1007/978-3-662-05291-4

http://www.springer.de

Originally published by Springer-Verlag Berlin Heidelberg New York in 2003.
Softcover reprint of the hardcover 3rd edition 2003

Cover design: de'blik, Berlin
Data conversion: PTP - Protago • TeX • Production, Berlin

Printed on acid-free paper 33/3142PS 5 4 3 2 1 0

It has turned out to be impossible ... to get at the meaning of these marks ... They refuse themselves to our understanding, and will, painfully enough, continue to do so. But when I say refuse, that is merely the negative of reveal – and that Nature painted these ciphers, to which we lack the key, merely for ornament on the shell of her creature, nobody can persuade me. Ornament and meaning always run alongside each other; the old writings too served for both ornament and communication. Nobody can tell me that there is nothing to communicate here. That it is an inaccessible communication, to plunge into this contradiction, is also a pleasure.

Thomas Mann, Doktor Faustus, III. Chapter: Jonathan Leverkühn contemplating a pattern on a New Caledonien sea shell. After the translation from the German by H. T. Lowe-Porter, Penguin Books.

Preface to the third edition

New in the third edition is that many of the simulations are supplied on the accompanying CD-ROM in the HTML format. Thus, the highly dynamic behavior of the interactions on which shell patterning is based can be inspected like conventional websites with any browser such as the Internet Explorer or Netscape. This is, of course, no longer restricted to PCs but also works on a Macintosh or Linux system. The animated simulations are given as separate files that also can be integrated, e.g., into a PowerPoint presentation if desired. Also included are animated simulations of models that describe more general problems in the development of higher organisms. These models were added in the second edition (chapter 12) and describe, e.g., formation of organizing regions, pattern formation in hydra, gene activation, formation of net-like structures, and chemotactic orientation.

The animated simulations are records of a particular simulation. By their very nature they do not allow changes of parameters, field size, modes of graphic display, etc. This, however, is possible with the PC-DOS programs supplied. They run on all the newer systems tested so far (Win9x, Win2000, XP-home edition). For systems that are unwilling to run the DOS programs, 32-bit emulators of DOS are available. A shareware version is included on the accompanying CD. Therefore, the programs should run on any modern Windows system. With a Windows emulator they also run on Macintosh computers.

For helpful corrections I am most grateful to Alfred Gierer and Sanjeev Kumar.

Hans Meinhardt

Preface to the Second Edition

As mentioned repetitively in the book, the models describing shell patterning are only special applications of a mechanism developed to account for biological pattern formation in general. To illustrate the close connection, a new chapter - originally written for the first German edition - has been added that provides a survey of these general models. Discussed is, for instance, how an embryo can obtain its primary axes, how gene activation can proceed under the influence of such signals in a position-dependent manner, how complex netlike structures such as the vein of leaves can be generated and how legs and wings are initiated during development at precise positions. Other sections of this chapter deal with phenomena at which the intimate connection to the mechanisms worked out for shell patterning are especially obvious. The utilization of travelling waves in blood coagulation, in the conduction of nerve pulses and in the chemotactic orientation of cells are examples. Close parallels between a shell pattern and phyllotaxis suggest an alternative view of how the helical arrangement of leaves is achieved.

Using the shell patterns as a natural exercise book, the computer program supplied with the first edition has been used in the meantime at several universities to teach students in basic properties of dynamic systems. I have been frequently asked to make the programs for general pattern formation available. The programs for the above mentioned models have been added to the accompanying diskette.

I am most grateful to Ute Grieshammer, Thomas Holstein, Lydia Lemaire, Florian Siegert, Ulrich Technau and Cornelius Weijer for supplying figures for the new chapter describing their experimental results. During the preparation of a German edition, Isolde Tegtmeier found several minor errors in the first edition that are now corrected. Jens Hemmen enabled some corrections in the nomenclature of shells. I thank Alfred Gierer and Thurston Lacalli for a critical reading of the new chapter.

Hans Meinhardt

Preface

The pigment patterns on tropical shells are of great beauty and diversity. They fascinate by their mixture of regularity and irregularity. A particular pattern seems to follow particular rules but these rules allow variations. No two shells are identical. The motionless patterns appear to be static, and, indeed, they consist of calcified material. However, as will be shown in this book, the underlying mechanism that generates this beauty is eminently dynamic. It has much in common with other dynamic systems that generate patterns, such as a wind-sand system that forms large dunes, or rain and erosion that form complex ramified river systems. On other shells the underlying mechanism has much in common with waves such as those commonly observed in the spread of an epidemic.

A mollusc can enlarge its shell only at the shell margin. In most cases, only at this margin are new elements of the pigmentation pattern added. Therefore, the shell pattern preserves a record in time of a process that took place in a narrow zone at the growing edge. A certain point on the shell represents a certain moment in its history. Like a time machine one can go into the past or the future just by turning the shell back and forth. Having this complete historical record opens the possibility of decoding the generic principles behind this beauty.

My interest in these patterns began with a dinner in an Italian restaurant. During the meal I found a shell with a pattern consisting of red lines arranged like nested W's. Since I had worked for a long time on the problem of biological pattern formation, this pattern caught my interest, more from curiosity. To my surprise it seemed that the mathematical models we had developed to describe elementary steps in the development of higher organisms were also able to account for the red lines on my shell. Thus, the shell patterning appeared to be just another realization of a general pattern forming principle. But this observation did not remain unchallenged for long. Soon thereafter I saw the complexity and beauty of tropical shells and realized that these patterns are not explicable on the basis of the elementary mechanisms in a straight forward manner.

We do not know what these patterns are good for. Presumably there is no strong selective pressure on the shell pattern. Variations are possible without severely influencing the viability of the animals. Since, as will be described in this book, the patterns result from the superposition of several pattern-forming reactions,

their diversity provides a natural picture book to study complex non-linear pattern formation.

To find models for these complex patterns turned out to be much more difficult than I thought. Of course, before making a simulation I was convinced that I had found the correct model. Using the simulation I learned frequently where mistakes in my thinking were and to what patterns my hypothesis really would lead. This led to new insights and new models. I am far from having a satisfactory model for every shell. But I hope that this book invites you to search for alternative and new solutions.

The book is accompanied by a computer program for performing the simulations on a Personal Computer. Most simulations shown can be reproduced. To see the emergence of these patterns on the screen provides a much more intuitive feel for the dynamics of the system. Since minor fluctuation can play a decisive role, even the repetition of the same simulation can lead to a somewhat different pattern. This corresponds to the fact that the patterns on any two shells are never identical. The program allows you to change parameters such as the life time of a substance or its spread by diffusion. The consequences of these changes can be seen immediately as an alteration of the pattern. The program is provided with full source code (Microsoft Professional, Quick or Visual Basic, Power Basic). Therefore, new model interactions can be easily inserted.

Acknowledgements

This book would not have been completed without encouragement from many quarters, foremost from my wife Edeltraud Putz-Meinhardt. I would like to express my thanks to those who contributed to the book. The basic ideas grew out of a theory I developed with Alfred Gierer. His concept of local autocatalysis and long ranging inhibition has been the basis of most of my work on biological pattern formation. Martin Klingler described in his master's thesis many interactions capable of reproducing shell patterns in fine detail. Discussions with Andre Koch and Kai Kumpf have been stimulating for me. I thank Drs. Ellen Baake, Jon Campbell, Christa McReynolds, Arthur Roll, Adolf Seilacher and Ruthild Winkler-Oswatitisch for shells and photographs. Christa Hug helped to prepare the manuscript, Karl Heinz Nill made the drawings, and Dr. Hans Wolfgang Bellwinkel brought the Thomas Mann-quotation to my attention. I am very grateful to Deborah Fowler and Przemyslaw Prusinkiewicz from the University of Calgary, Canada, for their contribution of the chapter on shell shapes (chapter 10) and Lynn Mercer for her very careful correction of the manuscript.

Last but not least, I am most grateful for the excellent working conditions provided by the Max-Planck-Institut für Entwicklungsbiologie in Tübingen over many years.

Hans Meinhardt

Contents