

## The Virtual Laboratory

Hans Meinhardt

# The Algorithmic Beauty of Sea Shells

*Fourth Edition*

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

With 148 Illustrations, 134 in Color,  
and CD-ROM

 Springer

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

*Series Editor*  
Przemyslaw Prusinkiewicz

ISSN 1431-939X  
ISBN 978-3-540-92141-7 e-ISBN 978-3-540-92142-4  
DOI 10.1007/978-3-540-92142-4  
Springer Dordrecht Heidelberg London New York

Library of Congress Control Number: 2009926970

© Springer-Verlag Berlin Heidelberg 1995, 1998, 2003, 2009

This work is subject to copyright. All rights are reserved, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilm or in any other way, and storage in data banks. Duplication of this publication or parts thereof is permitted only under the provisions of the German Copyright Law of September 9, 1965, in its current version, and permission for use must always be obtained from Springer. Violations are liable to prosecution under the German Copyright Law.

The use of general descriptive names, registered names, trademarks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

Springer-Verlag or the author make no warranty of representation, either express or implied with respect to this CD-ROM or book, including their quality, merchantability, or fitness for a particular purpose. In no event will Springer-Verlag or the author be liable for direct, indirect, special, incidental, or consequential damages arising out of the use or inability to use the CD-ROM or book, even if Springer-Verlag or the author have been advised of the possibility of such damages.

*Cover design:* deblik, Berlin

Printed on acid-free paper

Springer is part of Springer+Business Media ([www.springer.com](http://www.springer.com))

*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, Doctor 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

The pigment patterns on tropical shells are of great beauty and diversity. Their mixture of regularity and irregularity is fascinating. 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 mollusk can only enlarge its shell at the shell margin. In most cases, only at this margin are new elements of the pigmentation pattern added. Therefore, the shell pattern preserves the record of a process that took place over time 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 at 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 been working on the problem of biological pattern formation for a long time, this pattern caught my interest, more out of 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 yet 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 cannot be explained by the elementary mechanisms in a straightforward 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 nonlinear pattern formation.

Finding 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. However, I hope that this book invites you to search for alternative and new solutions.

The book is accompanied by computer programs for performing the simulations on a PC. Most simulations shown can be reproduced. Seeing these patterns emerge 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 produce a somewhat different pattern. This corresponds to the fact that the patterns on any two shells are never identical. The programs allow you to change parameters such as the half-life of a substance or its spread by diffusion. The consequences of these changes can be seen immediately as an alteration of the pattern. The programs are provided with full source code (FreeBasic for Windows/Linux; Microsoft QBX or QB, and PowerBasic for DOS). Therefore, new model interactions can be easily inserted.

## **What has been added in the new editions**

As mentioned already in the first edition, the models describing shell patterning are only special applications of mechanisms developed to account for biological pattern formation in general. To illustrate these close connections, in the second edition a new chapter was added in which models are discussed that describe, for instance, how an embryo can obtain its primary axes, how legs and wings obtain their own coordinate system at the correct positions, and how gene activation can proceed under the influence of graded signals in a position-dependent manner. We started our modeling with the freshwater polyp hydra. Meanwhile it turned out that these primitive organisms can be regarded, as far as the body plan is concerned, as living fossils that provide information of how the formation of body axes of higher organisms evolved. As explained now in Chapter 12, pattern formation in such simple organisms provides a key to understanding how of the body axes are established in higher organisms.

Models originally developed to describe some sea shell patterns turned out to provide a key to understanding other developmental systems, it turned out. Overtly the arrangement of leaves on a growing shoot, the patterning of bird feathers, the localization of the plane of cell division in a bacterium, blood coagulation, and the chemotactic orientation of cells seem to have little in common with patterns on a

sea shell. Now, in the fourth edition, a new chapter shows that these systems have a common logical basis. They depend on signals that become quenched shortly after they are generated. This leads to highly dynamic pattern-forming systems that never reach a stable state; avoiding to enter into a state in which the system is irreversibly trapped. Such flexibility then accounts for biological systems that require a permanent adaptation to changing situations.

To provide easier access to the highly dynamic behavior of the interactions on which shell patterning is based, animated simulations were added to the accompanying CD-ROM in the third editions. These can be inspected like conventional websites with any browser in any system. For most of these reactions only a single click is required to see the equations and parameters. The animated simulations are given as separate files that can be integrated, e.g., into a PowerPoint presentation if desired. Also included are animated simulations of models that describe general steps in the development of higher organisms, for instance, regeneration and transplantation experiments with hydra. In the fourth edition PowerPoint presentations were added for the major topics. They also contain many animated simulations.

The best way to become familiar with these reactions is to run these programs enclosed. They are written in the easy-to-use language BASIC. New on the CD of the fourth edition are versions that run under WINDOWS<sup>®</sup> and LINUX. The corresponding compilers are freely available on the Web and working versions are supplied. Since the source code is enclosed, too, new interactions can be easily added and their behavior can be investigated by running simulations, changing parameters, and performing ‘experimental’ manipulations. Moreover, it is now straightforward to save simulation results in a form that allows printing or integration into other applications.

## Acknowledgements

This book could 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 formed the basis of most of my work on biological pattern formation. In his diploma thesis Martin Klingler described 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-Oswatitsch for shells and photographs. Christa Hug helped to prepare the manuscript and Karl Heinz Nill made several of the drawings. I am very grateful to Deborah Fowler and Przemyslaw Prusinkiewicz from the University of Calgary, Canada, for contributing their chapter on shell shapes (Chapter 10). Lynn Mercer and Sherryl Sundell provided very careful corrections of the manuscript.

To prepare the later editions, I am most grateful to Hans Bode, Piet de Boer, Ute Grieshammer, Matthew Harris, Bert Hobmayer, Thomas Holstein, Lydia Lemaire, Richard Prum, Florian Siegert, Ulrich Technau, and Cornelius Weijer for supplying figures for the new chapters 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 provided some corrections in the nomenclature of shells. My son Christoph Meinhardt supported me with the LINUX - and C-implementation of the program. I thank Alfred Gierer, Thurston Lacalli, Sanjeev Kumar, and Afonso Guerra Assunção for a critical reading and comments. Very encouraging was the continuous support of Hermann Engesser and Dorothea Glaunsinger from the Springer Company.

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.



# Contents

<b>1</b>	<b>Shell patterns - a natural picture book to study dynamic systems and biological pattern formation</b>	<b>1</b>
1.1	Dynamic systems everywhere	1
1.2	Pattern formation	2
1.3	Dynamic systems are difficult to predict	3
1.4	Pattern formation in biology	4
1.5	Most shell patterns preserve a faithful time record	5
1.6	Elementary patterns: Lines perpendicular, parallel and oblique to the direction of growth	6
1.7	Oblique lines	8
1.8	Relief-like patterns follow the same rules	9
1.9	Many open questions and some hints	10
1.10	The hard problem: complex patterns	15
1.11	Earlier attempts to understand shell patterns	17
<b>2</b>	<b>Pattern formation by local self-enhancement and long range inhibition</b>	<b>19</b>
2.1	The activator – inhibitor scheme	19
2.2	Stable patterns require a rapid antagonistic reaction	20
2.3	Periodic patterns in space	21
2.4	The width of stripes and the role of saturation	25
2.5	Early fixation of a pattern	27
2.6	The activator - depleted substrate scheme	29
2.7	The influence of growth	30
2.8	Inhibition via destruction of the activator	32
2.9	Autocatalysis by an inhibition of an inhibition	33
2.10	Formation of graded concentration profiles	35
2.11	Pattern formation in two dimensions	38
<b>3</b>	<b>Oscillations and traveling waves</b>	<b>41</b>
3.1	The coupling between the oscillators by diffusion	44
3.2	The width of bands and interbands	47

3.3	Oblique lines: traveling waves in an excitable medium . . . . .	47
3.4	Traveling waves require a pace-maker region . . . . .	49
<b>4</b>	<b>Superposition of stable and periodic patterns . . . . .</b>	<b>53</b>
4.1	The formation of undulating lines and the partial synchronization of cells by activator diffusion . . . . .	54
4.2	Reducing wave termination with a longer activation period . . . . .	58
4.3	Interconnecting wavy lines and the formation of arches . . . . .	58
4.4	Hidden waves . . . . .	60
4.5	Pattern on the shell of <i>Nautilus pompilius</i> . . . . .	61
4.6	Stabilizing an otherwise oscillating pattern by diffusion . . . . .	62
4.7	Combinations of oscillating and nonoscillating patterns . . . . .	63
4.8	Rows of patches parallel to the direction of growth . . . . .	63
4.9	The possible role of a central oscillator . . . . .	66
4.10	Conclusion . . . . .	68
<b>5</b>	<b>Crossings, meshwork of oblique lines and staggered dots: the combined action of two antagonists . . . . .</b>	<b>71</b>
5.1	Displacement of stable maxima or enforced de-synchronization by a second antagonist . . . . .	71
5.2	Pattern variability . . . . .	73
5.3	Global pattern rearrangements . . . . .	74
5.4	Traces of the additional inhibition: oblique lines initiated or terminated out of phase . . . . .	76
5.5	Crossings and branching . . . . .	79
5.6	Changing the wave speed before and during collisions . . . . .	82
5.7	Parallel and oblique rows of staggered dots . . . . .	84
5.8	Conclusion . . . . .	89
<b>6</b>	<b>Branch initiation by global control . . . . .</b>	<b>91</b>
6.1	Branch formation: the trigger of backwards waves . . . . .	91
6.2	Simultaneous pattern change in distant regions . . . . .	93
6.3	No <i>Oliva</i> shell is like another . . . . .	98
6.4	The influence of parameters . . . . .	99
6.5	Alternative mechanisms . . . . .	100
6.6	A very different pattern generated by the same interaction . . . . .	101
<b>7</b>	<b>The big problem: two or more time-dependent patterns that interfere with each other . . . . .</b>	<b>105</b>
7.1	Inherent similarities in complex patterns . . . . .	105
7.2	White nonpigmented drop-like pattern on a pigmented background . . . . .	108
7.3	Evidence of a sudden extinguishing reaction . . . . .	110
7.4	Resolving an old problem with the separate extinguishing reaction . . . . .	111
7.5	The next step in complexity: an additional stabilizing pattern . . . . .	112

7.6	Branch formation by a temporary stabilization . . . . .	116
7.7	Intimate coupling of an enhancing and an extinguishing reaction . . . . .	119
7.8	Extinguishing that results from a depletion of resources due to an enhancing reaction . . . . .	121
7.9	Related patterns reveal unsolved problems . . . . .	123
7.10	Apparently different patterns can be simulated by closely related models . . . . .	126
7.11	Conclusion . . . . .	128
<b>8</b>	<b>Triangles . . . . .</b>	<b>131</b>
8.1	The crossing solution through the backdoor . . . . .	132
8.2	Triangle <i>versus</i> branch formation . . . . .	135
8.3	The involvement of three inhibitory reactions . . . . .	139
8.4	Breakdown as a failure of the enhancing reaction . . . . .	143
8.5	Conclusion . . . . .	145
<b>9</b>	<b>Parallel lines with tongues . . . . .</b>	<b>147</b>
9.1	Survival using a precondition pattern . . . . .	147
9.2	Tongue formation: refresh comes too late . . . . .	150
9.3	Variations on a common theme . . . . .	157
9.4	<i>Conus textile</i> : tongues and branches on the same shell . . . . .	159
9.5	Missing elements, missing links . . . . .	162
<b>10</b>	<b>Shell models in three dimensions . . . . .</b>	<b>167</b>
10.1	Mathematical descriptions of shell shape: a brief history . . . . .	167
10.2	Elements of shell shape . . . . .	168
10.3	The helico-spiral . . . . .	169
10.4	The generating curve . . . . .	171
10.5	Incorporating the generating curve into the model . . . . .	171
10.6	Modeling the sculpture on shell surfaces . . . . .	174
10.7	Shells with patterns . . . . .	179
<b>11</b>	<b>The computer programs . . . . .</b>	<b>187</b>
11.1	Introductory remarks . . . . .	187
11.2	Using the program . . . . .	187
11.3	GUIDED TOURS . . . . .	190
11.4	Implementation of the interactions . . . . .	190
11.5	Numerical instabilities that may cause errors . . . . .	192
11.6	Compilers and versions . . . . .	193
11.7	Parameters used in the program . . . . .	194
<b>12</b>	<b>Pattern formation in the development of higher organisms . . . . .</b>	<b>205</b>
12.1	Hydra, a versatile model system . . . . .	208
12.2	Tissue polarity and graded competence . . . . .	211
12.3	How to avoid periodic structures during growth . . . . .	212
12.4	How to generate structures at a distance: head and foot of hydra . . . . .	214

12.5	Induction of adjacent structures . . . . .	215
12.6	The evolution of the main body axes . . . . .	216
12.7	Gene activation under the control of a morphogen gradient . . . . .	219
12.8	Position-dependent activation of several genes . . . . .	221
12.9	A problem that the mollusks don't have: the initiation of legs and wings . . . . .	224
12.10	Conclusion . . . . .	228
<b>13</b>	<b>Pattern formation in development in which shell-related mechanisms are implicated . . . . .</b>	<b>231</b>
13.1	Arrangement of leaves and staggered dots on shells - two similar patterns . . . . .	231
13.2	Veins and nerves: the formation of net-like structures . . . . .	235
13.3	Chemotactic orientation of cell polarity . . . . .	239
13.4	Highly dynamic effects in preparing cell division in budding yeast . . . . .	242
13.5	Out-of-phase oscillations in <i>E.coli</i> bacteria for center-finding to determine the plane of cell division . . . . .	244
13.6	<i>Dictyostelium</i> : traveling waves at the border to multicellular organisms . . . . .	245
13.7	Feather patterns . . . . .	247
13.8	Color patterns of feathers . . . . .	248
13.9	Barbs of flight feathers are separated by traveling waves of local signals . . . . .	250
13.10	Nerve conduction as a traveling wave phenomenon . . . . .	251
13.11	Activation and extinguishing waves in blood coagulation . . . . .	252
	<b>References . . . . .</b>	<b>255</b>
	<b>Index . . . . .</b>	<b>265</b>

# Shell patterns - a natural picture book to study dynamic systems and biological pattern formation

## 1.1 Dynamic systems everywhere

Everyday we are confronted with systems that have an inherent tendency to change. The weather, the stock market, or the economic situation are examples. Dramatic changes can be initiated by relatively small perturbations. In the stock market, for instance, even a rumour may be sufficient to trigger sales, lowering quotations and causing panic reactions in other shareholders.

An essential element of dynamic systems is a positive feedback that self-enhances the initial deviation from the mean. The avalanche is proverbial. Cities grow since they attract more people, bacteria or viruses can replicate and the progeny start replicating too. In the universe a local accumulation of matter may attract more dust, eventually leading to the birth of a star.

Earlier or later self-enhancing processes evoke antagonistic reactions. A proliferating virus may trigger an immune response that neutralizes the virus. A collapsing stock market stimulates the purchase of shares at a low price, thereby stabilizing the market. The increasing noise, dirt, crime and traffic jams may discourage people from moving into a big city.

In addition to the balance between self-reinforcing and antagonistic tendencies, several other elements play a decisive role in the fate of dynamic systems. For instance, if the antagonistic reaction follows with some delay, the self-enhancing reaction can cause an overshoot or even an explosion. The explosion of dynamite is a good example. After ignition of a small portion the resulting heat and the shock wave ignite more of the explosives in the neighborhood. The reaction is so vehement because the oxygen required for burning is part of the chemical and is available immediately. Thus, no antagonistic effect slows down the reaction until the explosive is used up. Of course, afterwards a further ignition is impossible.

But let us consider a fire. Fire is also a self-enhancing process since more heat releases more burnable gases from the fuel. But the depletion of oxygen may represent an antagonistic reaction that keeps the fire down to the point that only smouldering is possible. In such a case, the rapid antagonistic reaction, the oxygen

depletion, hinders the development of a big fire. The burning process can go on for a much longer period although at a lower level. Thus the ratio of reaction times between the self-enhancing and the antagonistic processes plays a decisive role.

Another example should illustrate the same fact. As a rule, it takes about two days to fully develop an influenza but it takes about a week to get rid of it. Thus, it appears that our immune system responds too slowly when compared with the growth rate of the virus. Initially the virus proliferates in an avalanche-like manner and we become sick. But what appears at first as a misconception turns out to be an advantageous strategy. The slower responding immune system accumulates more and more specific antibodies until the entire virus can be trapped. The body can completely rid itself of the virus. If the immune system responded much faster, a balance between the proliferating virus and the immune system would be established at a lower level. The body would have to fight for the rest of its life against the ever proliferating virus since partial removal of the virus would lead to a corresponding down-regulation of the immune response, providing a new chance for the virus. With the system as it is, we are sick for a week, but after this week we are healthy again and free of the virus.

## 1.2 Pattern formation

Another decisive parameter in a dynamic system is the spread of its components. In the example mentioned above, the virus may be transmitted to another person who will also become sick after some delay. The infection spreads like a traveling wave. This spread is possible only since the self-enhancing agent, the virus, but not the antagonistic reaction, the immune response, can be transmitted to another individual.

In other systems, it is the antagonistic reaction that spreads more rapidly, and this can lead to stable patterns. Let us regard the formation of sand dunes in the desert (Figure 1.1). Dunes are formed despite the fact that the wind very quickly redistributes the sand. Dune formation may be initiated by a stone in the desert that provides a wind shelter. Sand accumulates behind the wind shelter, and a dune begins to grow. But the sand, once settled in the dune, cannot participate in dune formation somewhere else. The growth of a dune lowers the sand content in the air. The antagonistic reaction results from this removal of sand particles being moved by the wind, and has a long range effect. In this way, the probability of initiating new dunes and the growth of existing dunes in the surrounding area is reduced. In contrast, the increased accumulation of sand behind the wind shelter has a range comparable with the size of the dune. Thus, the basic elements for the formation of stable patterns are a short range self-enhancing reaction and a long range antagonistic reaction.

A similar argument can be made for the formation of valleys and rivers by erosion. The pattern of a ramified river system is certainly not preceded by a



**Figure 1.1.** The sand dune paradox. Naively, one would expect that the wind in the desert causes a structureless distribution of the sand. However, wind, sand and surface structure together represent an unstable system. Sand deposits more rapidly behind a wind shelter. This increases the wind shelter which, in turn, accelerates the deposition of more sand - a self-enhancing process.

corresponding pattern of rain fall, but results from a self-organizing process. The deepening of a valley proceeds essentially by the erosion of a meandering river. A larger valley collects water from a more extended portion of the surface. Thus, a larger valley has a better chance of becoming even deeper.

The antagonistic reaction can result from a depletion of material trapped by the self-enhancing process, such as in the sand dune example mentioned above. Alternatively, a direct inhibitory effect may spread out from such a self-enhancing center. In the formation of stars both effects play a role. A local increase of matter attracts more cosmic material - the self-enhancing process. One of the antagonistic reactions results from the depletion of cosmic dust in the surroundings. In addition, there is an active antagonistic effect produced by the developing star: the emitted light exerts a so-called light pressure that repels dust particles.

### 1.3 Dynamic systems are difficult to predict

Investigations of so-called chaotic systems have emphasized the fact that processes exist that are inherently unpredictable on the long term although each step is unequivocally determined by the preceding situation. The weather is an example. Calculation of future developments would require the knowledge of a given situation with an arbitrary precision - a knowledge that is impossible to obtain.

The situation is similar in the systems discussed above where strong positive feedback couplings are involved. Minute differences in the initial conditions can cause a completely different outcome if the situation is just on the border at which a

self-enhancing process becomes dominant. If self-enhancement is triggered in such a “revolutionary” situation, it will obtain a dynamic fairly independent of the mode of ignition.

If small differences are responsible for the selection of different pathways, our intuition of such systems is unreliable. Many attempts have been made to obtain a better understanding using mathematical modeling. For complex systems this is possible only using approximations since one can never be sure that all critical parameters have been considered. The problem becomes even more severe if the feelings and thinking of human beings have a strong influence on the fate of a system, as it is the case in politics or economy. The difficulty in making a prediction is obvious if even a rumour can induce a panic that is not justified by the real situation.

There are two main reasons for modeling dynamic systems: to provide a check on whether a system is fully understood, and to make predictions, at least for the near future.

To obtain the laws that govern a system, a comparison with its development in the past is an important check on whether a system is correctly understood, at least in retrospect. This requires good historical data.

Due to the importance of dynamic systems, on the one hand, and the difficulty of understanding them, on the other, it seems advisable to study relatively simple model systems. A very particular model will be discussed in the present book - the patterns on the shells of mollusks. These motionless calcified patterns are more reminiscent of artistic decorations on china than dynamic systems. However, a closer inspection of many shells reveals dramatic events in their history.

## 1.4 Pattern formation in biology

The generation of patterns on the shells of mollusks is, of course, only a very special case of the general problem of how an organism obtains its complex structure during development. The life cycle of a higher organism starts, as a rule, with a single fertilized cell. At the end of embryonic development a very sophisticated arrangement of highly specialized cells is generated. The similarity of identical twins is an indication of how stringent this process is under genetic control. But reference to genes does not provide an explanation of this process *per se* since, as a rule, with each cell division both daughter cells obtain the same genetic information.

It appears to be a hopeless enterprise to find a mathematical description (and thus an unequivocal understanding) of a process as complex as the formation of a higher organism. However, it turns out that this process can be separated into many steps that can be regarded, as a first approximation, to be independent of each other. For instance, a very important process for a developing embryo is the formation of the primary embryonic axes. Some signals must be present to determine where to form a head, tail and so on in the initially more or less uniform (usually hollow) sphere of cells. It turns out that for the fruit fly *Drosophila*, for instance,



the anteroposterior axis (head to tail) is under the control of a completely different set of genes than the dorsoventral (back to belly) axis (Nüsslein-Volhard, 1991). Another example of the independence of a structure from the surrounding tissue is the formation of legs. After its initiation, an amphibian leg develops fairly normally even after transplantation to an ectopic position. Its development proceeds under the control of a local coordinate system. Because of this partial independence one can make models of the individual elementary steps. Of course, the steps must be linked together in order to position the individual structures in correct relation to each other. For instance, in a developing organism it is essential that the head-to-tail and the back-to-belly axes are arranged perpendicular to one another, but this is already a refinement. These issues will be discussed in detail in chapter 12.

We have proposed several models of biological pattern formation for specific developmental situations (Gierer and Meinhardt, 1972, Gierer, 1981, Meinhardt, 1982). It came as a surprise to me that the patterns on the shells of mollusks could be described with basically the same equations that were initially derived to describe elementary steps in biological pattern formation, such as the formation of embryonic axes, the head formation of the freshwater polyp *Hydra*, or the initiation of periodic structures such as leaf formation at the tip of a growing shoot. Thus, the shell patterns will be used as a natural picture book to become more familiar with a general mechanism that is the basis for a very important process, biological pattern formation.

## 1.5 Most shell patterns preserve a faithful time record

In normal development, a strong evolutionary pressure exists to reproduce a given structure faithfully. Moreover, a structure, once formed, usually remains stable at least for a certain time interval. In contrast, the functional significance of the pigment patterns on shells is not clear. Many mollusks live buried in the ground; some are covered with an opaque layer, the periostracum that disappears only after the death of the animal. One hypothesis is that mollusks dispose waste products into their shells (Comfort, 1951). In this view, it would be unimportant whether pigment depositions occur in certain time intervals, permanently at regular distances or in waves that move periodically over the shell-producing mantle gland. Thus, presumably there is no strong selective pressure on a particular shell pattern. The diversity indicates that it is possible to modify the pattern drastically without endangering a species. Nature is allowed to play.

Shells consist of calcified material. The animals can increase the size of their shells only by accretion of new material at the margin, the growing edge. In Figure 1.12 later in this chapter the edge of a shell is clearly to be seen. Most decorations of shells result from the incorporation of pigments during this growth process. Once made, as the rule, the patterns remain unchanged. The patterns are therefore



**Figure 1.2.** Different modes of pattern formation on shells of *Cypraea diluculum*. The banding pattern results during the growth of the shell by the sequential addition of new material. The pattern is a time record of a linear pattern forming process taking place at the growing edge. The dot-pattern around the opening results from a two-dimensional pattern forming process at later stages. The snail engulfs its shell by an ectodermal protrusion in which the corresponding pattern is generated. Pigment produced in this layer becomes deposited on the shell.

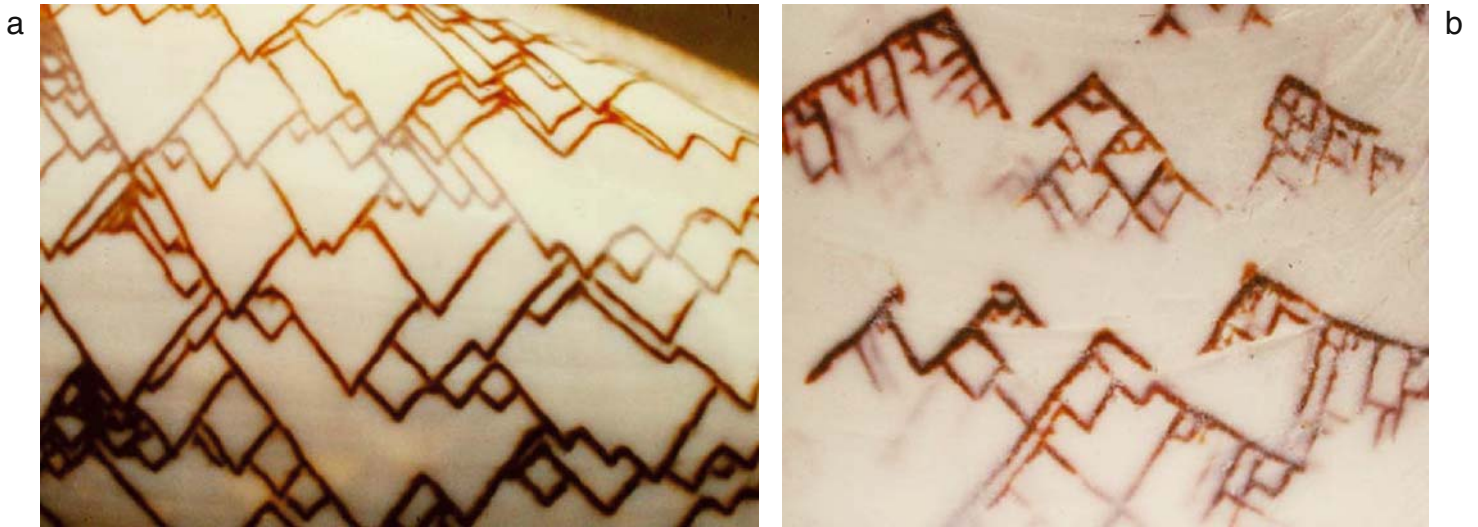
historical records of what happens at the growing edge, i.e., they are a time record of a pattern forming process in a more or less linearly arranged array of cells.

Some shells, however, produce their pattern in a totally different way. Ectodermal protrusions engulf the shells and pattern forming processes within these sheets are copied onto the shell. Thus, in these cases pattern formation results from a two-dimensional process. The pattern represents a snapshot of a particular moment, not a time record. Some snails change from one mode to the other after reaching adulthood. On the shell of *Cypraea diluculum* (Figure 1.2) one can see both types of patterns on the same shell. While the juvenile pattern consists of oblique lines, the later pattern formed around the shell opening consists of isolated dots. Although the patterns look so different, we will see that they can be explained by basically similar mechanisms.

For the purpose of the book, the first type of patterns, those that are generated over the course of time, are most interesting since they bear the historical record of their formation. They provide therein a key for deciphering the underlying pattern forming process. I will deal mostly with this type of pattern.

## 1.6 Elementary patterns: Lines perpendicular, parallel and oblique to the direction of growth

Shells show an enormous diversity of patterns whereby related species can show very different patterns while nonrelated species can show very similar patterns. The shells shown in Figure 1.3 provide an example: one shell belongs to a snail, the



**Figure 1.3.** Similar pattern on nonrelated mollusks. Details of the shell patterns of *Oliva porphyria* (left) and the bivalved mussel *Lioconcha hieroglyphica*. Both patterns consist of branching oblique lines. The branching occurs frequently at the same level on distant lines indicating that control of branch initiation is a nonlocal process (see Figure 6.1)

other to a bivalved mussel. Both shells show oblique lines that branch. They share a very characteristic element. The initiation of several branches occurs frequently at the same horizontal level, i.e., it can take place simultaneously at distant positions, a feature that will be discussed later in detail. The similarity in nonrelated species indicates that the different patterns are generated by a common mechanism and that the diversity is generated by minor modifications.

To find an inroad into the logic behind these patterns, it is advisable to start with more elementary patterns. Figure 1.4 shows shells with lines parallel and perpendicular to the direction of growth. Keeping in mind the space-time character of the shell pattern, lines parallel to the direction of growth indicate the formation of a spatial periodic pattern of pigment production along the edge that is stable in time. At more or less regular distances, groups of cells in the mantle gland produce permanent pigment while cells in between never do so. This is the usual situation in morphogenesis where particular structures such as leaves, hairs or feathers become initiated at regularly spaced positions.

Other patterns indicate that pigment deposition oscillates. A particular cell produces pigment only during a certain time interval and then enters into an inactive (refractory) period until the next pigment producing phase occurs. A synchronous oscillation in pigment production leads to stripes parallel to the axis. In the example given in Figure 1.4 it can be clearly seen that the oscillations are almost but not completely synchronous. Some regions of the edge are white, others are pigmented. Thus, the synchronization cannot be a result of external influences, like daily or seasonal fluctuations, in contrast to the situation, for instance, in tree rings.



**Figure 1.4.** Elementary pattern: stripes parallel and perpendicular to the direction of growth. In the upper shell pigmentation has occurred at regular time intervals more or less synchronous. Axial stripes (i.e., stripes perpendicular to the direction of growth) result. In the lower shell pigmentation occurred permanently at regularly spaced positions leading to stripes parallel to the direction of growth.

The mechanisms that lead either to synchronous oscillations or to a stable pattern in space cannot be very different from each other. The specimen at the bottom of Figure 1.4 has on its cone a pattern resulting from oscillations while the main pattern was generated by a stable system. As shown below, a change of the ionic strength in the water can be sufficient to cause a corresponding pattern alternation (see Figure 1.11).

## 1.7 Oblique lines

Oblique lines originate from traveling waves of pigment production. Such waves arise if pigment-producing cells trigger their neighboring cells so that - after a certain delay - these cells also start to produce pigment and so on, analogous to the formation of the influenza wave mentioned earlier.

Pure elementary patterns - stripes parallel, perpendicular or oblique to the growing edge - are more the exception than the rule. For instance, the perpendicular lines in the lower shell of Figure 1.4 show small gaps at regular intervals suggesting that



**Figure 1.5.** Bulges instead of pigmentation: elementary patterns of the relief type showing ripples parallel, perpendicular and oblique to the direction of growth. These ripples have a biological function; they increase the friction of the shell in the sand or mud.

an oscillating pattern was superimposed. The branching of the oblique lines shown in Figure 1.3 indicates that the traveling waves involved in shell patterning can have unusual properties. At a certain moment, a wave can split producing a wave that moves backwards - a process that never occurs, for instance, in a nerve pulse that travels along a nerve fibre.

## 1.8 Relief-like patterns follow the same rules

Pigmentation is not the only possible decoration on shells. Relief-like structures are also very frequent. The same elementary patterns as listed above occur. Figure 1.5 shows corresponding examples.

As a rule, relief-like patterns are less complex and more reproducible from specimen to specimen. Relief-like patterns also have biological functions. For bivalved mussels, the rough surface increases the friction with the sand during the opening and closing of the two shells and facilitates in this way burrowing into the sand or mud. As shown by paleontological work (Seilacher, 1972), species that originally appear different can develop towards similar shapes and surface structures if they populate the same habitat and are forced to behave in a similar way. Therefore, in contrast to pigmentation patterns, relief-like patterns seem to be shaped by strong selective pressure.

## 1.9 Many open questions and some hints

Very little is known about the mechanisms that lead to shell patterning. The models worked out in this book can only describe which type of interaction could in principle account for such patterns. No information can be obtained about the chemical nature of the substances involved. Sometimes two different models can reproduce the natural counterpart with reasonable agreement. Usually, however, related species with similar patterns are available that can be described much better by one or the other mechanism. Therefore, the model's handling of natural variability provides one of the criteria for its quality.

Some shells show very particular features that are helpful in getting ideas about the underlying mechanism. Some examples will follow.

Occasionally shells show an obvious perturbation of the normal pattern. A traumatic event must have happened in the animal's history such as temporary dryness, lack of food or injury by a predator. After such a perturbation, the pattern may be very different for a long period. There is strong support for a model that is able to account not only for the normal pattern but also for the pattern regulation after such a perturbation. Several examples will be given later on.

Since the shell grows in several rounds around the axis, parts of the progressing shell formation are in direct contact with parts formed in a previous round. On some shells oblique lines extend from an older (inner) region to a newer (outer) winding without major discontinuity (Figure 1.6). This indicates that an existing pigmented region, if touched by a growing mantle gland, can initiate a traveling wave of pigment production on the newly formed portion of the shell. The result is that both stripes appear in register. These snails can "taste" the old stripe. Such tasting has been proposed by Ermentrout *et al.* (1986) for other reasons, namely to account for the sometimes very long periods in the oscillation of pigment depositions.

A very interesting phenomenon can be seen on the right shell of Figure 1.6. There, only every second oblique line is in register with an old line. Obviously, the spontaneous oscillation frequency was too high during the last round of growth. Only every second initiation of pigment production could be triggered by the old pattern while in between a spontaneous trigger took place.

Similarly, on bivalved mollusks, a synchronization can take place between shells such that the two shells become mirror-symmetric to each other. Figure 1.7 shows two pairs. Obviously, some cross-talk took place between the two shell-producing mantle glands. If one produces pigment, the other produces pigment too. This, however, takes place only if relatively coarse patterns are generated. If more detailed patterns are formed, both patterns may have common features but the details may be different. Figures 5.1 and 5.8 show two complementary and more complex shells.

Sometimes it is difficult to decide what is pattern and what is background. The two shells in Figure 1.8 show dots. One shell carries pigmented dots on



**Figure 1.6.** An existing pigment pattern can trigger the formation of a new one. Oblique lines are frequently in register on parts of the shell that have been formed during the preceding round of shell growth. The arrows mark some instances. This can only be interpreted by the assumption that in the pigment-forming mantle gland the previously deposited pigmentation is detected, which activates, in turn, the new pigmentation. In these cases, traveling waves are initiated. In the right shell only every second line continues (arrows).



**Figure 1.7.** Mirror-symmetry in bivalved shells of mollusks. Some cross-talk must take place between the two shell-producing glands such that pigment formation on one shell triggers pigment formation on the other. Finer patterns have common features but are different in the details.



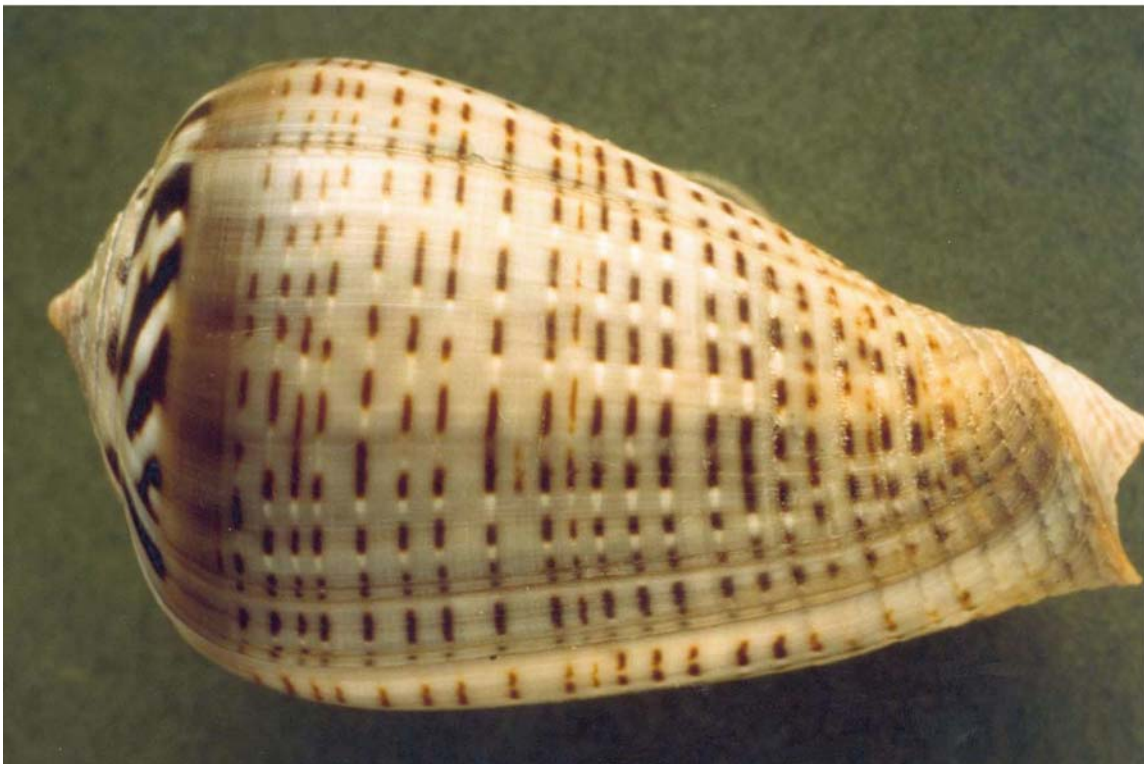
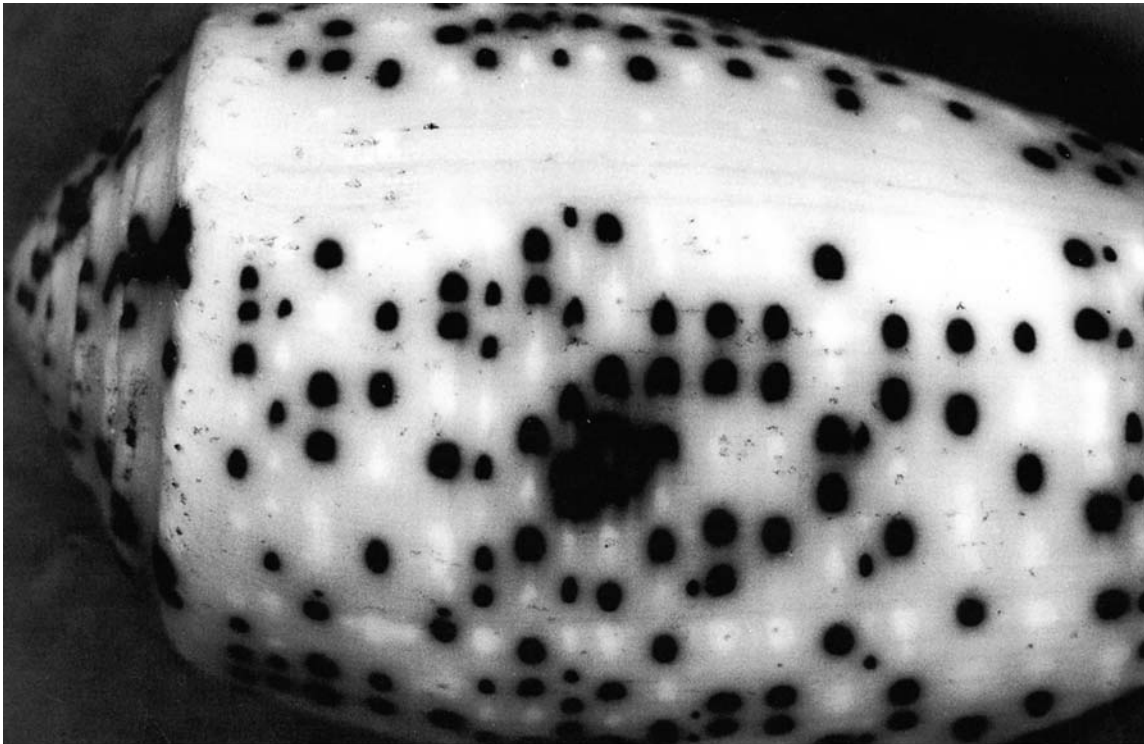
**Figure 1.8.** Figure and ground: Staggered dots in reverse pigmentation on *Babylonia papillaris* and *Neritina natalensis*. Finer details, for instance, the dark border at the lower edge of the white patches (insert) indicate that the two patterns depend on different mechanisms.

less-pigmented background; on the other shell the situation is the reverse. The similarity could indicate that a common mechanism generates a signal, but the two mollusks make different use of that signal. In one case the signal promotes, and in the other case the signal inhibits pigmentation.

However, a detailed inspection reveals more differences. The unpigmented patches on the right shell show narrow, very dark borders at their lower edge and the pigmented background has a fine structure of densely packed narrow lines. It is an extreme form of a general pattern that will be treated in detail further on (see Figure 9.7). The common feature is the offset of a particular pattern element along the space and time coordinates. But this feature can be achieved by several mechanisms that differ in their degree of complexity.

Other shell patterns indicate that two interacting systems are involved. For instance, on the shell of *Conus zeylanicus* (Figure 1.9) rows of dark, crescent-like patches are visible. The patches within a row are at very irregular distances from each other. A closer inspection reveals that the irregularity results from a random alternation of the pigmented patches with patches that are significantly less pigmented than the light gray background. Thus, two signals seem to be produced, one that causes pigmentation and another one that suppresses pigmentation. The irregularity excludes the idea that the dark and white patches result from a single oscillating system at different stages of the cycle. However, some coupling between the two systems must exist since the dark and the white spots always keep a certain distance from each other.

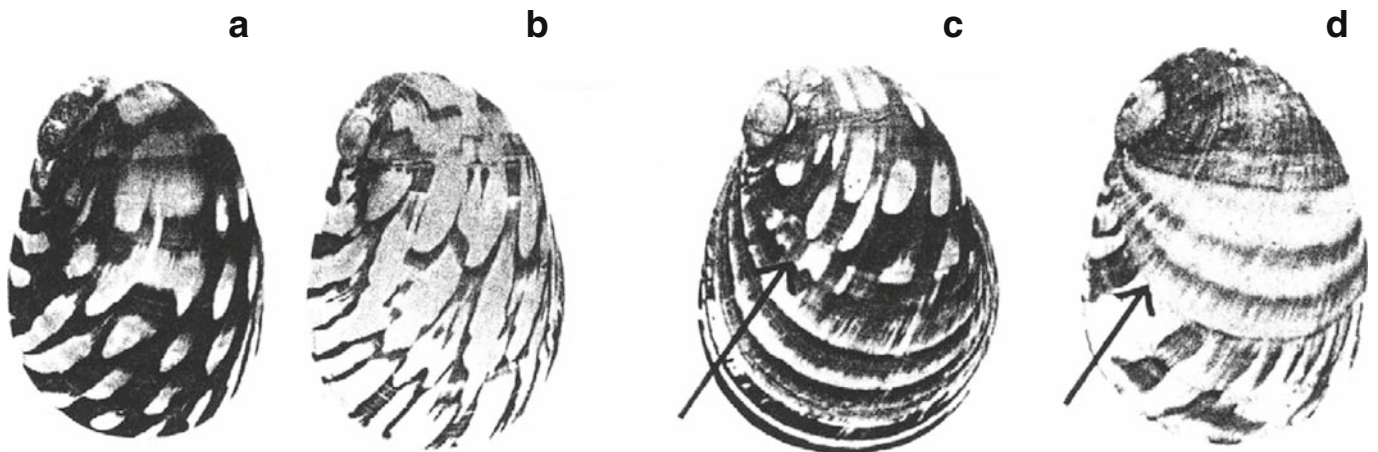




**Figure 1.9.** Alternation of dark and white regions. The alternating pattern is restricted to particular stripes. On the upper shell, *Conus zeylanicus*, dark pigmentation and pigmentation lighter than the grey background alternate in a more irregular fashion. On the bottom shell this alternation is more regular, although some brown stripes are not followed by a white stripe. These patterns indicate the involvement of two different signal systems, one that enhances and another that suppresses pigmentation.



**Figure 1.10.** Global oscillations and pigmentation pattern. The modulation of the background in the left shell indicates a global oscillation that controls or synchronizes the dark pigmentation, causing the ladder pattern. In the right shell some pigmentation lines are occasionally shifted against each other. This indicates the absence of global control. Also no background modulation is visible. Thus, even in related species the pattern forming mechanism can be different. The synchronizing influence of a global oscillation on pigment deposition is responsible for several other phenomena (see Figure 4.14).



**Figure 1.11.** Modification of shell patterns by changes in the ionic strengths. (a, b) Variants of a fresh water snail with dense and sparse shell pigmentation, kept at low ionic strengths. (c, d) Dramatic pattern modifications after changes in the salt concentration in the aquarium, either from low (freshwater) to high salt concentrations (0.37%) or (d) from high to low salt concentrations. Arrows indicate the time of change. (Photographs kindly supplied by D. Neumann, see Neumann, 1959b)

Another example where a faint pigmentation provides some hints of the mechanism is given in Figure 1.10. Parallel lines are framed by oblique lines, providing an overall impression of connected triangles. A closer inspection of the yellowish background reveals that there is a modulation in the same phase as the dark horizontal lines. Obviously, a global oscillation exists that acts either as a precondition or it modulates the oscillation that causes the darker pigmentation. As a note of precaution, the second shell of Figure 1.10 is a related species with a similar pattern. In this shell, however, the horizontal lines are partially out of phase. No synchronization by a global oscillation and no modulated background can be seen. Therefore, even in related species it is dangerous to generalize too much.

Little experimentation has been reported with shell patterns. The pattern of the freshwater snail *Theodoxus fluviatilis* depends on the salt concentration (Neumann, 1959a-c). In Germany, waste water with high salt concentrations from potassium mining is introduced into the river Werra. He found pattern changes downstream from the waste water dispersal. These pattern changes can be reproduced in the laboratory. Figure 1.11 shows the pattern after a shift from high to low salt concentrations and *vice versa*. Obviously, there is no strong regulatory system in the animal to maintain its typical pattern. To the contrary, all the examples mentioned above indicate that the pigment-producing system is very sensitive. A change in the external conditions, an influence from pigmentation laid down earlier or from the shell counterpart can modify pigment production.

## 1.10 The hard problem: complex patterns

Many shells show highly complex patterns. The shell of *Conus textile*, Figure 1.12, provides an example. The complexity is not without rules. Some regions show a light brown, others a white background. Darker oblique lines are visible whose general characters depend on the background, more faint in the white but thicker in the light brown region. Moreover, there is a strong tendency to change from parallel lines (synchronous oscillation) in the brown region to oblique lines (traveling waves) that branch in the white region. Keeping the space-time character in mind, it is clear that the transition from white to brown is preceded by a dark brown line, while the brown-white transition is not. The faint oblique lines in the white region frequently have their origin in a thick dark line in the brown region. The brown-white transition occurs usually simultaneously in an extended region, causing a light brown white border parallel to the edge.

This complexity cannot result from a single pattern-forming reaction. Two or more reactions must be superimposed that influence each other. Usually only one pattern, the pigmentation, is visible. A second pattern that modifies the pigmentation pattern may be invisible but must be deduced from the unusual behaviour of the pigmentation pattern. In the case of *Conus textile* the light brown pattern is presumably an exception in that a visible trace of the second pattern



**Figure 1.12.** An example of a complex pattern: *Conus textile*. Two pigmentation systems appear to be superimposed. Light brown pigmentation occurs preferentially in two bands that cover large regions. In addition oblique lines with a much darker pigmentation exist. The dark pigmentation system is influenced by the light one. In the light brown region the dark brown pigmentation lines are much thicker and are preferentially oriented parallel to the growing edge. In regions with nonpigmented background the dark lines are much narrower.

system exists. The different behaviour of the pigment system - synchronous oscillations *versus* traveling waves depending on whether the light brown pattern is in the ON or OFF state - suggests general modifications of one system by the other. The problem in understanding complex patterns lies in the enormous number of combinatorial possibilities between two or more systems. Each component of one system can activate or suppress another; the influence may involve changes in the production or destruction rates; and so on. The simulation of the complex patterns provided in this book should be regarded only as an attempt to decipher the complex interaction and as an invitation to search for other possibilities.