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

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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©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.

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