REVIEWS

Coquillages de Djibouti by Alain Coulombel, 1993, Editions Edisud, La Calade, RN7, 13090 Aix en Provence, France. 143 pp. ISBN 2-85744-707-8. Available from the Publishers, price 260 Francs (approx. £29).

This book serves as a good introduction to the Marine shells of Djibouti, a small state at the mouth of the Red Sea, between Ethiopia and Somalia and opposite to Aden. As France is the former colonial power it is fitting that this study should have been published in France. The text is in French, but illustrations explaining the specialist terms used in the descriptions help make it easy to follow. The introduction includes details of local habitats and a section on conservation and it is interesting to note that such a small state should have two Marine National Parks.

The bulk of the book consists of detailed descriptions of the species covered - some 200 Gastropods and 40 Bivalves - accompanied with superb quality colour photographs, most life size or larger, showing dorsal and ventral views of each Gastropod and interior and exterior views of each Bivalve. Maps clearly show the local distribution of each species and there is an indication of the frequency with which each shell occurs in Djibouti, There is no indication of the species wider distributions outside Djibouti and the use of local frequency only can be confusing — *Cypraea moneta,* for example, is considered rare and *Cypraea pulchra* abundant The number of species covered is limited concentrating on those larger species which will more commonly be found, and it is a pity that many smaller species occurring in the area are not included. There are, however, a number of unusual species illustrated. I was particularly interested in the selection of Ancillas which includes *A. testudae, A. djiboutina, A. albisulcata, A. acuminata, A. ventricosa, A. exigua* & *A. ampla.* A number of Red Sea endemics are prominently featured, including *Cypraea exusta, Mitra bovei, Conus erythraeensis* and *Homalocantha digitata,* but it is surprising to find the locally common subspecies *Strombus gibberulus albus* shown as *S. gibberulus.*

The large format - 25 cm x 29 cm - make the book a little unwieldy to handle, it could certainly not be used as a field guide, but it is well laid out and easy to use with a good bibliography and index. It can certainly be recommended as a good introductory guide to the shells of Djibouti but is limited in coverage.

Kevin Brown

The Algorithmic Beauty of Sea Shells By Hans Meinhardt, 1995. Berlin: Springer - Verlag. xi + 204 pp., with 121 illustrations, mostly in colour, and 3.5" disk. Hardback. ISBN 3-540-57842-0. Price £31.45.

This beautifully produced book manages to delight the eye whilst efficiently explaining elegant hypotheses for the amazing diversity of striking patterns found on mollusc shells. The explanations are ultimately in terms of reaction-diffusion equations, but no mathematics is needed to follow the arguments. A simple example of the kind of model is of one substance, the activator, that promotes production both of itself and of another substance that inhibits production of the activator. This can cause the concentration of activator to vary in a wave-like manner, undulating either in space or in time, this depending on the relative diffusion and decay rates of activator and inhibitor. Meinhardt envisages that at each point along the strip of mantle tissue around the shell aperture the concentration of activator determines whether pigment is produced. The beauty of molluscs is that as the shell grows it lays down a historical record of how the distribution of pigment production changes. Reaction-diffusion equations are much invoked in the embryology of other organisms, so the audience for this book should not be restricted to malacologists.

Although the more involved models in the later chapters do inevitably require more concentration, the writing is clear, helpfully structured and never plodding. Occasional allusions to such non-molluscan phenomena as sand dunes, candles and the economy, are not only fun but also illuminating. The algebra is restricted to a few boxes, whilst the main text explains the output of the models intuitively. The numerous colour illustrations, of excellent shell photographs side-by-side with the graphical output of the computer; models, are closely integrated with the text and helpfully amplify the explanations. Really the book would be worth buying just for the illustrations, since, even if one has no interest in underlying mechanisms, the book is valuable as a catalogue of the diversity of patterns. An added bonus is that a disk is included containing the program that generated nearly all the outputs illustrated. It is straightforward to run on any IBM compatible computer, the parameters for each published illustration can be read from the disk, then these parameters can be altered or, if you really do get involved, the original source code is provided.

Is there good evidence for the mechanisms proposed by Meinhardt? No direct physiological evidence of activator or inhibitor substances exists. With some shell patterns the simplicity of Meinhardt's explanatory mechanism is appealing, but other simple mechanisms have also been proposed, such as neural interactions[1]. In those shells in which stripes on adjacent whorls are entrained, it seems likely that some neural mechanisms do need to be involved. One paragraph mentions some such "rival" models, but by no means all relevant papers are cited and I was disappointed that the opportunity was not taken to review the different approaches. For instance there is another school of modelling shell patterns based on cellular automata, and I remain unsure to what extent this is just an alternative way of describing the same processes. For comments on the successes and failures of these two schools, readers might look at the 1996 paper by Kusch & Markus[2].

With more complex patterns, Meinhardt has to resort to more complex models, sometimes with so many parameters that one wonders whether jiggling their values could generate any pattern, and thus whether the model is untestable. However, what I found convincing was that it was not just the broad patterning that could be made to fit, but that sometimes fine details of the shapes emerged as strikingly concordant with reality. Meinhardt does not rely just on general similarity to define what is an adequate model, but comments, for instance, on the pattern following growth disruptions, or on intraspecific variation, and he checks whether patterns in related species could be generated by related models. Unfortunately virtually no experimental manipulations have tested Meinhardt's hypotheses, or anybody else's.

One example illustrated is the banding in *Cepaea*. This set me wondering, because we know something of the genetics of shell pattern in *Cepaea* and some other land pulmonates[3]. Could one relate the genetics to the substances and parameters hypothesised in the model? Even when the genetics is poorly understood, a more quantitative analysis of intraspecific variation would provide a more stringent test of the model. This should be combined with a quantitative sensitivity analysis involving altering each of the model's parameters. Perhaps this was done but only occasional qualitative results are mentioned. A formal sensitivity analysis also gives the data on which to base a classifcation of patterns; it is possible that apparently quite different patterns could result from a small change in a single parameter. Another issue also interests me: if Meinhardt's model of standing waves is correct, can particular bands on *Cepaea* be counted as homologous when the total number of bands differs?

The *Cepaea* example further stimulated me to question Meinhardt's complacent belief that "Presumably there is no strong selective pressure on shell pattern". He contrasts pigment patterns with shell sculpturing whose much greater consistency in pattern is ascribed to stronger selection pressures. I am worried about the claim of non-adaptation, because the polymorphism in *Cepaea* used to be dismissed as non-adaptive[4], yet experiments have since demonstrated many adaptive consequences[5]. Some shell patterns provide such an exquisite historical record of the regularity of an individual's development that one might even predict that they should be used in mate choice! The beautiful *Clithon* shells illustrated in the book have a complex pattern of parallel lines and paler "tongues", and, although the precise patterning may not matter, the overall graininess certainly made them cryptic to me in the wild. Unfortunately, and mysteriously, many ornately patterned shells are said always to be covered up in life by sediment or an opaque coating. But rather than assuming neutrality Meinhardt could utilise his models to provide evidence of adaptation: ask what patterns that the models can generate are not observed in the wild[6].

The last main chapter is not written by Meinhardt but attempts to integrate his shell patterning models with three-dimensional models of shell growth. This is potentially an important exercise since at parts of the shell near the coiling axis the growth rate is much slower and the direction of growth is almost perpendicular to that around the rest of the aperture. A blank shell cannot simply be wrapped up in the flat designs printed elsewhere in the book. But, disappointingly, this chapter introduces few new insights. The model used, the logarithmic helicospiral, is descriptive, which contrasts with the philosophy of the rest of the book of building up from a mechanism with the aim of understanding the mechanism. Some suggestions about mechanistic modelling of shell growth do exist in the literature[7], but probably this would have been too ambitious a task here. Unfortunately when the modelled shells are displayed next to their real counterparts, the agreement in shape around the columella is in several cases distractingly imperfect. Nevertheless the chapter does contain one delightful idea: a virtual-reality museum in which one can explore a gallery of beautiful computer-generated shells. Unlike in real museums we could inspect a shell from as close as we like—even from inside.

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[5] JONES J.S., LEITH B.H. & RAWLINGS P. 1977 Polymorphism in Cepaea: a problem with too many solutions. *Annual Review of Ecology and Systematics* **8**: 109–143.

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[7] HUTCHINSON J.M.C. 1989 Control of gastropod shell shape; the role of the preceding whorl. *Journal of Theoretical Biology* **140**: 431–444.

[7] MORITA R. 1991 Mechanical constraints on aperture form in gastropods. *Journal of Morphology* **207**: 93–102.

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