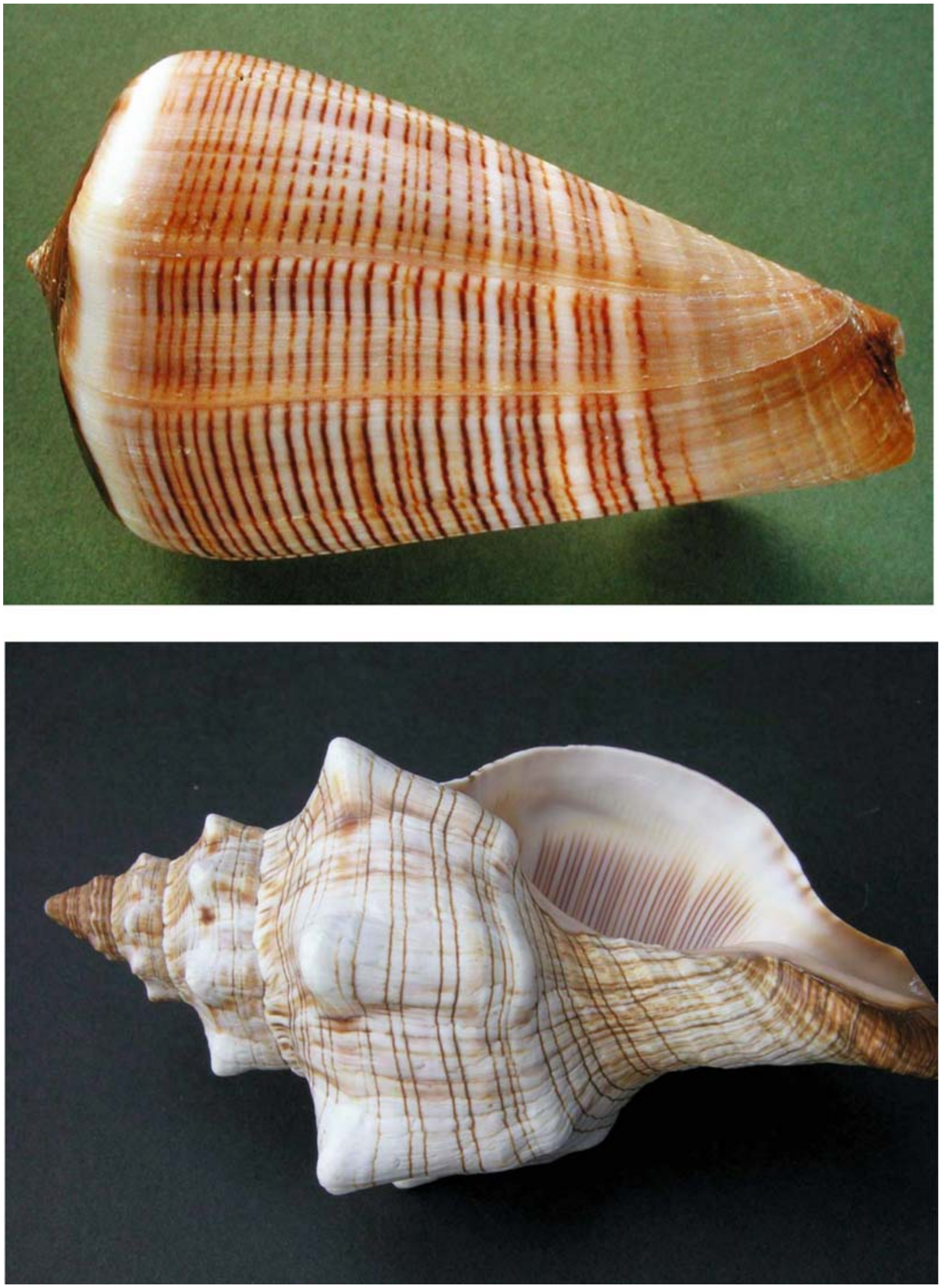

Figure 2.1. Patterns stable in time and their traces on shells. Stripes perpendicular to the growing edge, i.e., parallel to the direction of growth, result from stable pigment production at a particular position and its suppression at locations in between. In the lower shell, different sets of stripes are formed on the inner and the outer surface of the shell. On the outer pattern, the stripes are formed in pairs. An explanation for this phenomenon will be given in Figure 2.4f. (*Conus loroiisi*, top, and *Neptunea lyrata*)

Chapter 2

Pattern formation by local self-enhancement and long range inhibition

Like other biological processes pattern formation is based on the interaction of molecules. In order to find a mathematical description for a particular process the concentrations of the substances involved must be described as a function of space and time. This is possible by using equations that describe the *changes* in concentration over a short time interval as a function of other substances. Adding these concentration changes to given initial concentrations provides us with the concentration at a somewhat later time. Repetition of such a calculation provides the total over the course of time. Three factors are expected to play a major role in the concentration change: the rate of production, the rate of removal (or decay), and the loss or gain due to an exchange with neighboring cells, for instance by diffusion.

As mentioned earlier, we have proposed that pattern formation starting from initially more or less homogeneous conditions requires local self-enhancement coupled with a long range antagonistic effect (Gierer and Meinhardt, 1972, Gierer, 1981, Meinhardt, 1982). Patterns are formed because small deviations from a homogeneous distribution create a strong positive feedback which causes the deviations to grow even more. A long-range antagonistic effect restricts the self-enhancing reaction and causes a localization.

2.1 The activator – inhibitor scheme

The scheme of a biochemically feasible realization of this general principle is shown in Figure 2.2. A short-range substance, the activator, promotes its own production (autocatalysis) as well as that of its rapidly diffusing antagonist, the inhibitor. The concentrations of both substances can be in a steady-state. A general increase in the activator is compensated by an increase in the inhibitor concentration. However, such an equilibrium is locally unstable. Any *local* increase of the activator will increase further due to autocatalysis despite the fact that a surplus of inhibitor is also produced by this local increase. It diffuses rapidly into the surroundings and slows down the autocatalysis while the local activator elevation increases further (Figure 2.2). A set of partial differential equations is given in Equation 2.1

H. Meinhardt, *The Algorithmic Beauty of Sea Shells*, 4th ed. The Virtual Laboratory,
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