Figure 3.1. Parallel and oblique lines, the traces of synchronous oscillations and traveling waves. On the shell of *Amoria ellioti* (top), the stripes are more or less perpendicular to the direction of growth. They result from an almost synchronous alternation between pigment producing and nonproducing phases. It is remarkable that the distance between the lines remains constant in regions of different shell diameter. Although the lower left pattern (*Nerita communis*) looks similar on the picture, it has a different origin. From the lower right figure it becomes clear that the stripes are oriented oblique to the direction of growth. Therefore, a pigmented region has triggered a neighboring region and so on, forming traveling waves at regular intervals. Minute irregularities and finer changes in the pigmentation indicate the orientation of the growing edge at the corresponding stage.

Chapter 3

Oscillations and traveling waves

A very important class of shell patterning is caused by pigment productions that occur only during a short time interval, followed by an inactive period without pigment production. Stripes parallel to the growing edge and oblique lines belong to this class of patterns. Such oscillations can occur if the antagonist reacts too slowly. Then, a change in activator concentration is not immediately back-regulated since the antagonist reacts too slowly and the activation will proceed in a burst-like manner. Only after a sufficient accumulation of the inhibitor, or after a severe depletion of the substrate, will activator production collapse. A refractory period will follow with very low activator production in which either the excess inhibitor will degrade or the substrate will accumulate until a new activation becomes possible. The condition for oscillatory activations is the reverse of that given for stable patterns. In an activator-inhibitor scheme, oscillations occur if the decay rate of the inhibitor is smaller than that of the activator i.e., if the condition $r_b < r_a$ in Equation 2.1 (page 23) is satisfied.

In the activator-depleted substrate model, oscillations occur if the rate of substrate production is too low to maintain activator production in a steady state, i.e., if $b_b < r_a$ in Equation 2.4 (page 28). The onset of oscillations in a depletion-driven system can be observed using an everyday experiment. If a thick candle burns for a while, a deep hole will form in the wax and the flame will begin to flicker. The reason is that the oxygen supply becomes insufficient for a large flame. The flame shrinks, consuming less oxygen, thereby allowing the oxygen concentration to recover and the flame becomes larger again; and so on.

Depending on the parameter, this reaction can exhibit different behaviors. A cell may become activated with an internal periodicity. Or, it may be arrested in an excitable state. Small changes in a parameter can lead to a transition from one to the other mode. Figure 3.2a, for instance, shows the switch between oscillations and stable activation occurring in a single cell that is caused by a change in the decay rate of the activator. Theories on oscillations and waves in excitable media are well developed (see, for instance, Prigogine and Lefever, 1968; Winfree, 1980; Segel, 1984; Glass and Mackey, 1988; Murray, 1989). The different modes will be discussed here in some detail since they are the tools for deducing the parameters required for the patterns observed on shells.

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