



**Figure 5.1.** Staggered dots on *Babylonia papillaris* and oblique lines with crossings on *Tapes literatus*. Although the patterns look very different, it is proposed that both are based on a common mechanism. Two antagonists enforce a periodicity in space and time

## Crossings, meshwork of oblique lines and staggered dots: the combined action of two antagonists

Many shells display simple periodic patterns that cannot be accounted for with the elementary mechanisms described so far. Patterns of staggered dots and meshworks belong in this class (Figure 5.1). These patterns are characterized by a periodicity along the time coordinate as well as along the space coordinate. This suggests that two antagonists are involved: a nondiffusible one that is responsible for the periodicity in time, and a second highly diffusible one that causes the pattern through space. The interactions described in this chapter are possible extensions of the activator-substrate and the activator-inhibitor model (see boxes). An important property of such mechanisms is that traveling waves can emerge without pace-maker regions and that colliding waves can penetrate each other without annihilation. In other words, crossings of oblique lines can occur.

### 5.1 Displacement of stable maxima or enforced de-synchronization by a second antagonist

For a more intuitive understanding of the role of the second antagonist let us first regard the elementary pattern on its own and then take the action of the second antagonist into consideration. If the primary system would lead to a stable pattern (highly diffusible antagonist), the local accumulation of the second antagonist would destabilize the maxima over the course of time. A neighboring region, not subject to the nondiffusible antagonistic effect, would become activated. Traveling waves would emerge.

Conversely, a system that is able to generate traveling waves (nondiffusible antagonist) may oscillate in a synchronous manner as long as no pace-maker region is available (see Figure 3.7a). An additional antagonist with a long range would enforce a de-synchronization. If a cell becomes activated somewhat later than its neighbors, this phase difference will increase during subsequent oscillations. The inhibitory influence that spreads from the advanced neighbors delays the somewhat retarded cells even more. The synchronism breaks down and traveling waves are formed. This type of transition is clearly visible in Figure 5.2.