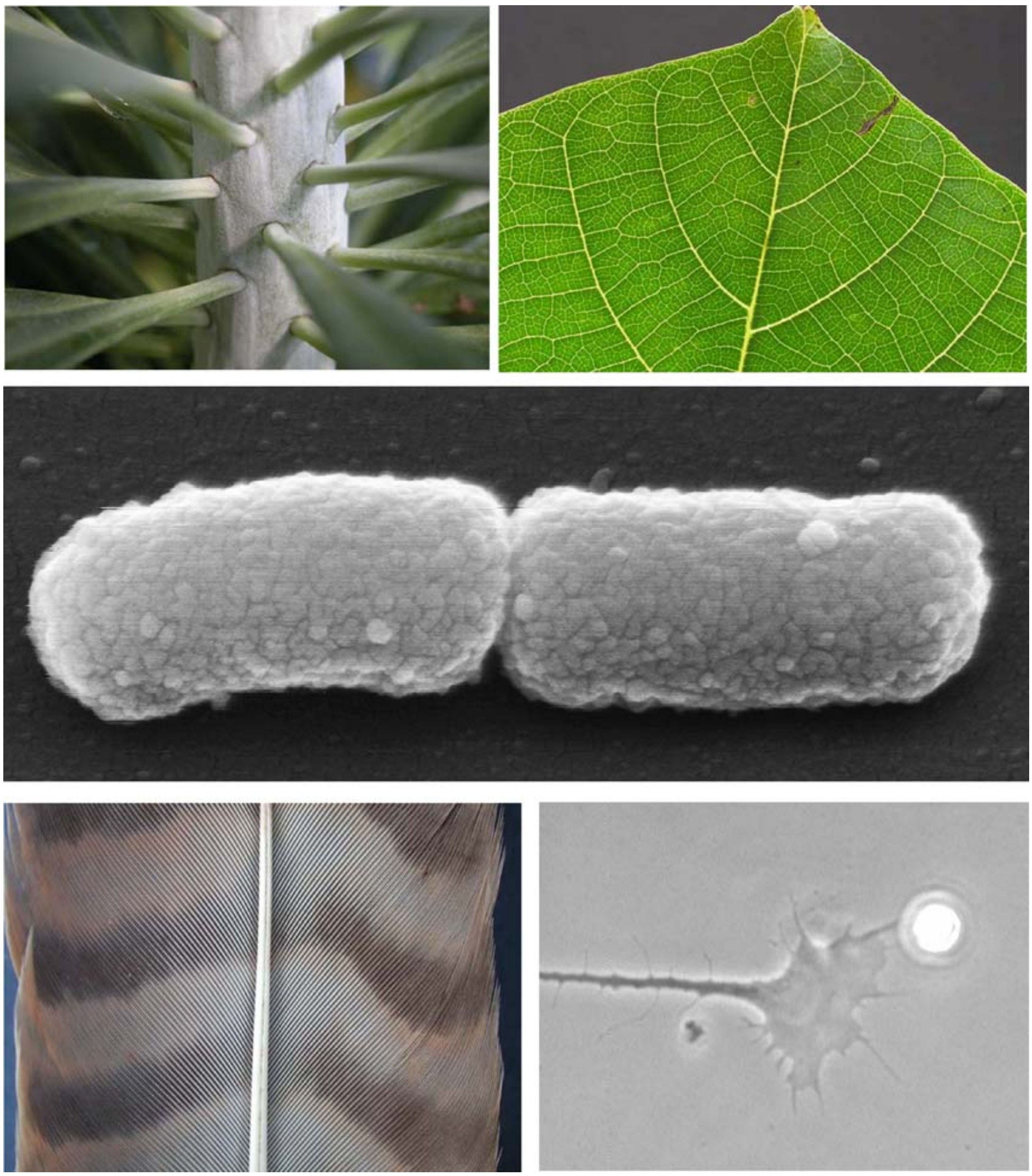

Figure 13.1. Helical arrangement of leaves, net-like structures, cell division in *E.coli*, barbs of feathers, and orientation of moving cells: quenching of signaling peaks shortly after their generation plays a crucial role in diverse biological systems

Chapter 13

Pattern formation in development in which shell-related mechanisms are implicated

Many shell patterns can be explained by the assumption that peaks of signaling molecules are locally quenched shortly after they emerge. As shown in Chapter 5, this can lead either to traveling waves or to maxima, which disappear and reappear at more or less regularly displaced positions. In this chapter it will be shown that this mechanism is not restricted to shell patterning. Processes as diverse as the patterning of the barbs of avian feathers, determining the center of an *E.coli* bacterium to localize the initiation of cell division, orienting the movement of chemotactic cells or growth cones, and initiating of leaves in a helical arrangement are based on closely related mechanisms (Figure 13.1). To correlate the molecular mechanisms found for these systems with the hypothetical mechanisms deduced from the shell patterning it will be necessary to use the more or less arbitrary names of genes and other components. I hope that this 'jargon' will not be too frustrating for those not familiar with the field. To discuss the mechanisms, however, the components need names.

13.1 Arrangement of leaves and staggered dots on shells - two similar patterns

The regular arrangement of leaves, the so-called phyllotaxis, has fascinated people for centuries (for a recent review see Canales et al., 2005; Kuhlemeier, 2007). At first glance, leaf initiation seems to have nothing in common with the patterning on sea shells, but this impression is misleading. In both cases, the new elements appear only in a narrow stripe-shaped zone and the emerging patterns are time records of pattern-forming reactions that took place in these generative zones. The tip of a shoot, called the apical meristem, contains rapidly dividing cells. Cells just leaving this central zone become competent to form new leaves. The competence is present only for a short time; no further leaves are initiated in cells that left this zone. Thus, the zone in which leaf initiation can take place has the geometry of a narrow ring that surrounds the central meristem (Figure 13.2a).

Each plant has its own characteristic phyllotactic pattern. Leaves can appear at opposite positions in an alternating sequence (180°, distichous patterns), in pairs

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