eighteenth century, which he observed by gently pouring an oil onto the surface of a pond. He took to carrying oil in a little vial in his walking stick, and would merrily create a miniature oil slick on every pond he encountered, particularly that on London's Clapham Common. What amused him was that just the tiny volume of oil that he carried would spread across the entire pond, and as it did so it would lower the surface tension of the water surface and leave it smooth as a mirror. I don't recommend trying this, however, unless you fancy you can explain to a park attendant that you are reproducing a historical experiment by Ben Franklin.

The study of surfactant films (particularly those of the soap-like molecules called fatty acids) on the surface of water was pioneered by Lord Rayleigh at the end of the nineteenth century and by the American chemist Irving Langmuir and his students at the beginning of the twentieth century. These films now bear the name Langmuir films, and they exhibit an astonishing range of pattern-forming behaviour. Langmuir created them in a shallow trough in which a movable barrier skimming the water surface allowed him to marshal the surfactant molecules into an ever smaller area of water surface and so control their density—which is to say, the average surface area commanded by each. As this density increases, a Langmuir film can undergo abrupt changes that are two-dimensional 'flatland' versions of the transformations from gas to liquid to solid that a material in three dimensions will undergo as it is compressed. But these films have an extra state: there are *two* kinds of 'flat' liquid, in both of which the molecules are mobile and disordered but which have distinctly differ-

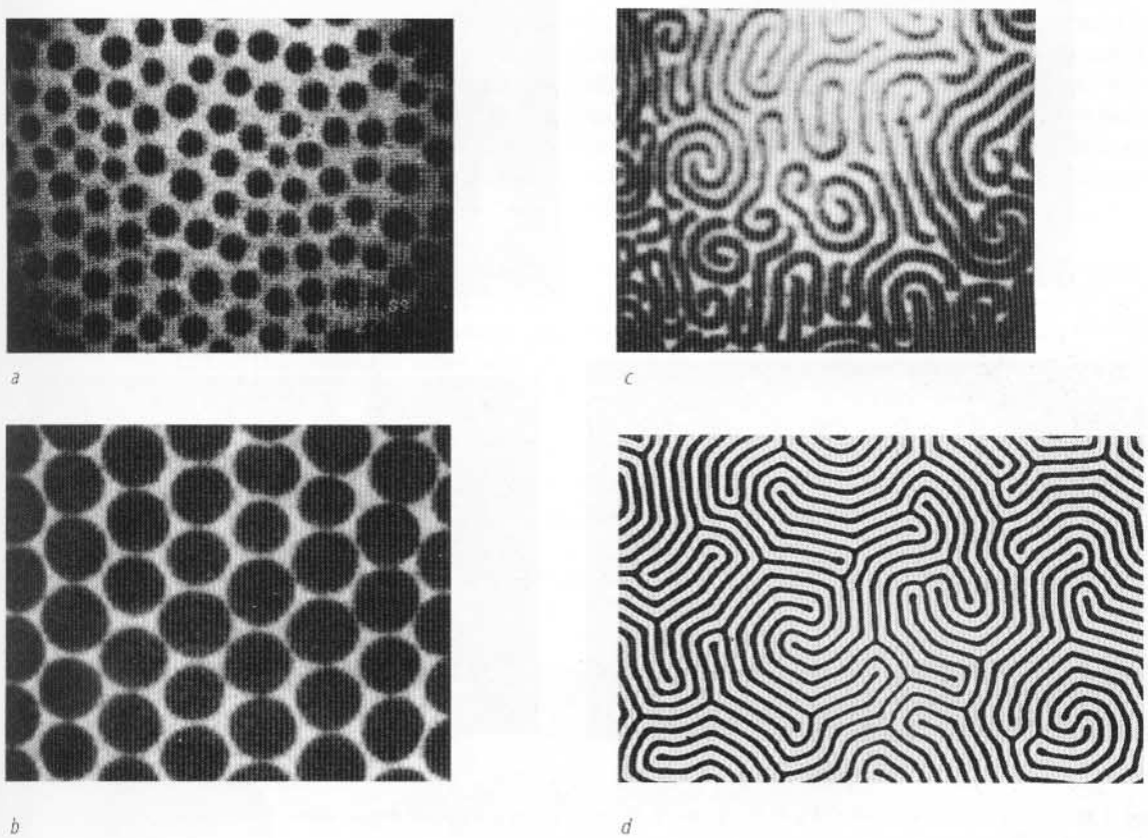
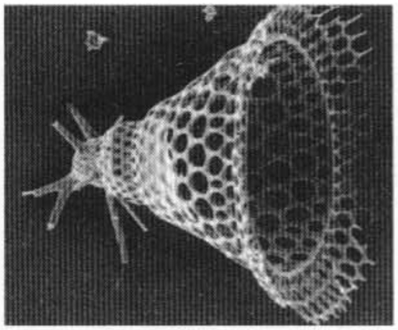
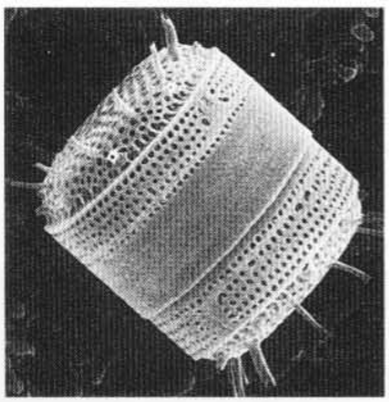


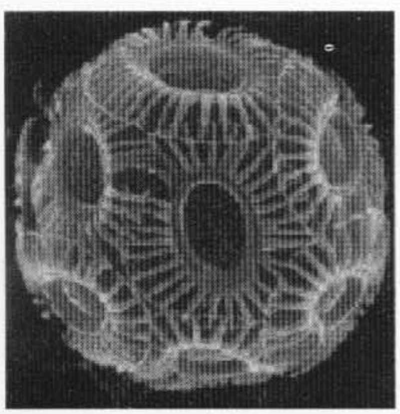
Fig. 2.21 Surfactants at the water surface will form a variety of different states when the surface layer is compressed. (*a*) A dense, disordered liquid-like state (called the LC state, *dark patches*) grows within a less-dense state (LE) that contains a fluorescent dye (*light regions*). (*b*) As the LC domains grow, they become ordered in a hexagonal pattern. (*c*) Eventually the LC domains become squeezed into worm-like shapes by their mutual repulsion. (*d*) The stripe phase of surfactant films is analogous to the striped arrangement of magnetic domains in thin films of garnet. Here too the stripes arise from mutual repulsion of the domains. (Photos: (*a*) S. Akamatsu and E. To, University of Paris IV; (*b*) Helmut Möhwald, Max Planck Institute for Colloid and Interface Science, Berlin; (*c*) Charles Knobler, University of California at Los Angeles; (*d*) Michael Seul, BioArray Solutions, Fanwood, New Jersey.)



a



b



c

Fig. 2.34 The skeletons of radiolarians (*a*) and diatoms (*b*) are thought to be the mineralized casts of a froth of vesicles. Coccolithophores (*c*) also have delicately patterned plates shaped by organic tissues. (Photos: (*a*) The Museum of Science, Boston; (*b*) Dee Breger, Lamont-Doherty Earth Observatory; (*c*) Jeremy Young, Natural History Museum, London.)

cells called osteoblasts, which deposit the hard stuff amongst the membranous web of organic tissues. Far more dramatically, the shells of marine organisms such as radiolarians and diatoms are the casts of patterns formed by ephemeral membranes and vesicles packed into foams (Fig. 2.34).

To scientists interested in pattern formation, these microscopic follies have surely been the most inspirational of life's constructions. And no wonder—for in both their beauty and their diversity, they are the biological equivalent of snowflakes. But as the biologist Karl von Frisch points out, nature is indifferent to aesthetics. 'I do not want to wax philosophical about so much "useless" beauty scattered over the oceans', he says, 'Nature is prodigal.'

The structures are not, strictly speaking, shells at all, but rather exoskeletons—external skeletons that enclose the soft, organic tissues of their architects. Several classes of marine organisms construct exoskeletons. Radiolarians are tiny, single-celled animals (protozoans) whose exoskeletons are made of silica. Diatoms, dinoflagellates and coccolithophores, on the other hand, are members of the class of microscopic plants called phytoplankton. Diatoms and dinoflagellates live mainly in coastal and polar waters, and their exoskeletons are also made of silica; coccolithophores are more abundant in warmer, tropical seas, and they make their elaborate cages from calcium carbonate, the fabric of chalk and marble.

When Christian Gottfried Ehrenberg made the first recorded observation of coccolithophores in 1836 while inspecting chalk from an island in the Baltic Sea, he thought that they must be inorganic mineral formations of some kind. All Ehrenberg saw were the 'bones'—oval-shaped platelets of the hard exoskeletons of these creatures preserved in the rock, their organic tissues having long since decayed. Ironically, while today those searching for ancient forms of fossilized microorganisms run the risk of being misled by complex mineral formations of organic appearance formed without the aid of living creatures (Chapter 1), Ehrenberg was initially deceived in the other direction: he could not imagine that the elaborate carbonate structures he found could have anything to do with life, and decided instead that they must be related to previously known spherical crystals called spherulites. Ehrenberg spent 14 years recording thousands of different forms of coccolith skeletons in meticulous drawings, all the time under the impression that he was drawing curious crystals.

In 1857 the biologist Thomas Huxley observed similar 'rounded bodies' in the muddy sediment pulled

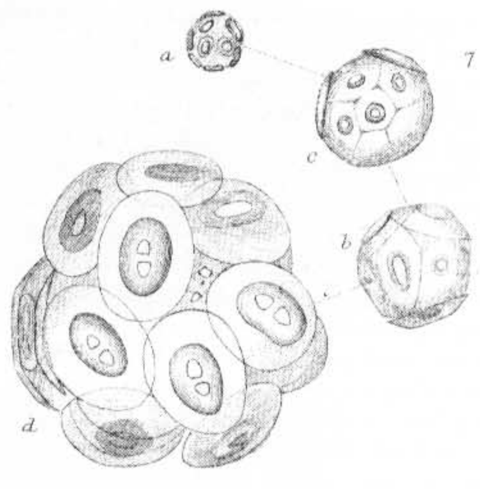


Fig. 2.35 Thomas Huxley sketched many coccoliths in 1868, but believed them to be inorganic formations. (Image: Jeremy Young, Natural History Museum, London.)

up from the deep North Atlantic Ocean. Although he noted that they looked 'Somewhat like single cells of the plant *Protococcus*', he too decided that they must be inorganic in origin, and he called them coccoliths (from the Greek *lithos*, stone) (Fig. 2.35). But in 1861, G.C. Wallich found these same oval-shaped platelets in seafloor sediments, and noticed that sometimes they were stuck together in spherical aggregates like those that Huxley sketched. These 'coccospheres' were often associated with plankton called foraminifers, and so Wallich decided that they were probably of biological origin. At the same time, the Englishman Henry Clifton Sorby came to the same conclusion after studying coccoliths in chalk. When Wallich and Sorby published their findings, most biologists, including Huxley, came to accept the biological origin of coccoliths. But not Ehrenberg, who resolutely maintained that they were inorganic until his death in 1876.

Huxley took a close look at his coccolith samples under a microscope, and observed that many were embedded in a transparent jelly-like slime, a 'protoplasm' of the sort identified a few years earlier by the German biologist Ernst Haeckel. He decided that the coccospheres were skeletal structures that helped to support this slime. Although it later became clear that the jelly was simply a product of chemical reactions between the sea water and alcohol used to preserve the specimens, in 1898 George Murray and V.H. Blackman proposed that the coccospheres are the protective armour of protoplasmic organisms—coccolithophores—that dwell within.

Much of what was known at this time about coccoliths and radiolarians came from the sediment samples collected by the British research vessel *HMS Challenger*, which from 1872 to 1876 embarked on a cruise to probe the secrets of the abyssal ooze. Ernst Haeckel was captivated by the geometric wonders of *Challenger's* bounty, and he catalogued hundreds of radiolarian exoskeletons in a vast Atlas (Fig. 2.36). Whereas coccolithophore shells are generally composed of overlapping, disk-shaped platelets, radiolarian exoskeletons are typically an ornate latticework of geometric polygons, with hexagons being particularly prominent. Haeckel's drawing of the organism *Aulonia hexagona* (Fig. 2.37*a*) showed a perfect sphere traced out in a web of hexagonal cells. But when, around the beginning of this century, D'Arcy Thompson came to exercise his awesome interpretive faculties on Haeckel's atlas, he noted something important: 'No system of hexagons

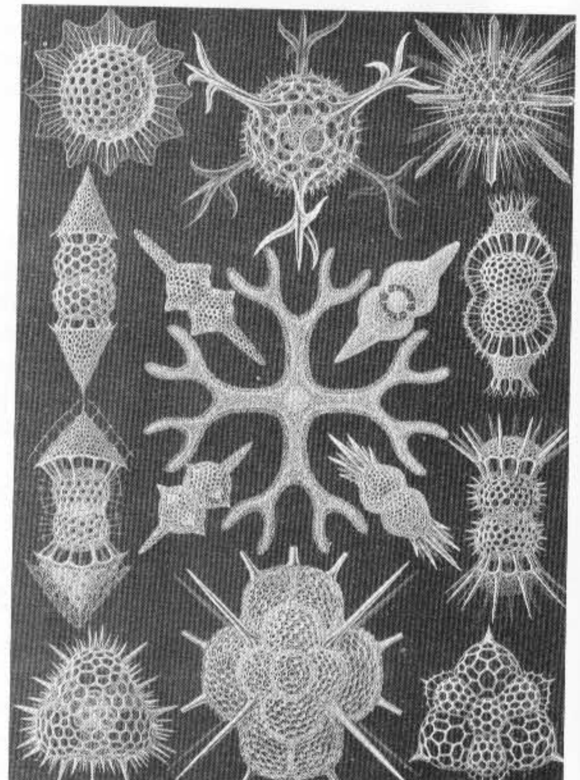
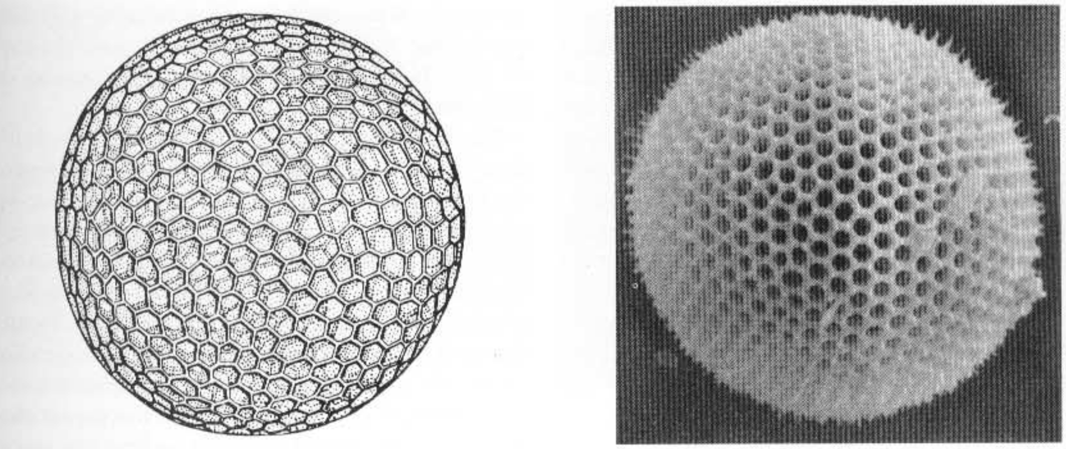


Fig. 2.36 The Atlas prepared by Ernst Haeckel depicts a vast selection of beautiful radiolarian skeletons.

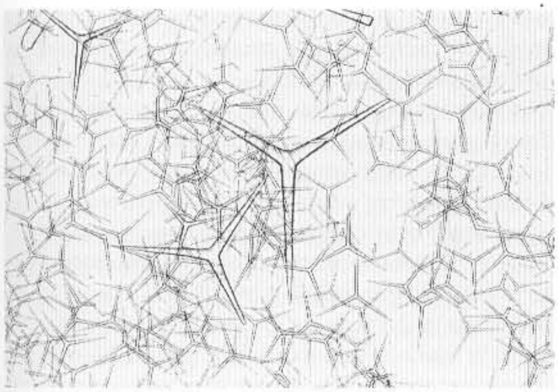


a b

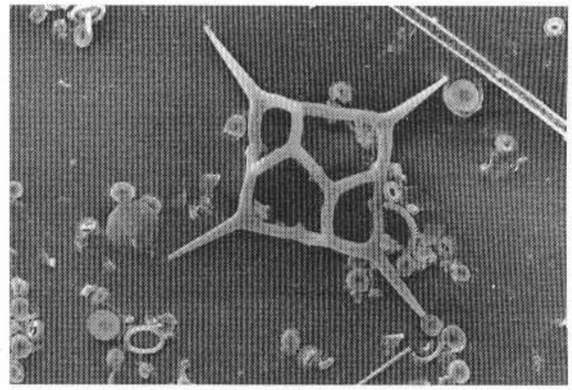
Fig. 2.37 The radiolarian *Aulonia hexagona* as drawn by Haeckel (*a*) and as it appears in the electron microscope (*b*). The shell is a closed sphere of primarily hexagons, but pentagons are also needed for closure. A few of these can be discerned in both images. (Images: (*a*) from Thompson 1961; (*b*) Tibor Tarnai, Technical University of Budapest.)

can enclose space… the array of hexagons may be extended as far as you please, … but it never closes in'. This, Thompson pointed out, was a consequence of a relationship deduced by mathematician Leonhard Euler between the number of faces, vertices and edges of a polyhedron. Euler's formula tells us that such a polyhedron cannot be made of hexagons alone. Instead, Thompson realized, there must be pentagonal or square facets in such a polyhedron to allow it to form a closed shell. Precisely 12 pentagons will suffice to close a polyhedral shell whose other faces are all hexagons, no matter how big the shell is. And indeed, said Thompson, Haeckel did allude to the presence of some pentagonal and square cells in the framework of the *Aulonia*

Fig. 2.38 Richard Buckminster Fuller used hexagonal and pentagonal elements to construct his geodesic domes, most notably that used in the US exhibit for Expo '67 in Montreal. (Photo: Copyright 1967 Allegra Fuller Snyder, courtesy of the Buckminster Fuller Institute, Santa Barbara.)



a



b

Fig. 2.40 (*a*) The spicules of sponges appear to represent the casts of Plateau borders between a few vesicles. (*b*) Plateau junctions are clearly evident in the exoskeleton of this silicoflagellate (compare Fig. 2.9). (Photos: (*a*) Michelle Kelly-Borges, Natural History Museum, London; (*b*) Stephen Mann, University of Bath.)

vesicles sometimes themselves become patterned with fine ornamentation that is transferred to the mineral platelet: a mesh of pores, presumably from the packing of smaller vesicles, is quite common on coccoliths.

We can see a particularly striking example of biomineral patterning in the skeletons of the sea-urchin *Cidaris rugosa*. The skeleton is a regular mesh of calcite (Fig. 2.41), which bears a remarkable resemblance to the cubic P-surface (see Fig. 2.28). It seems most likely that the organic tissues within which the mineral is originally deposited have conspired to adopt a structure very much like this periodic minimal surface, which acts as a template for skeleton formation. The smooth, continuous curvature of the mineral means that it can distribute loads evenly and is not liable to split along the atomic planes of the crystal. As a consequence, skeletons like these can attain strengths greater than that of reinforced concrete. So there are clearly practical benefits to these complex patterns.

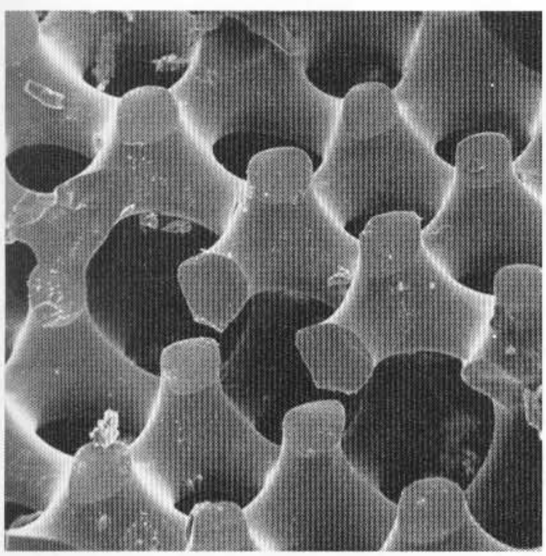
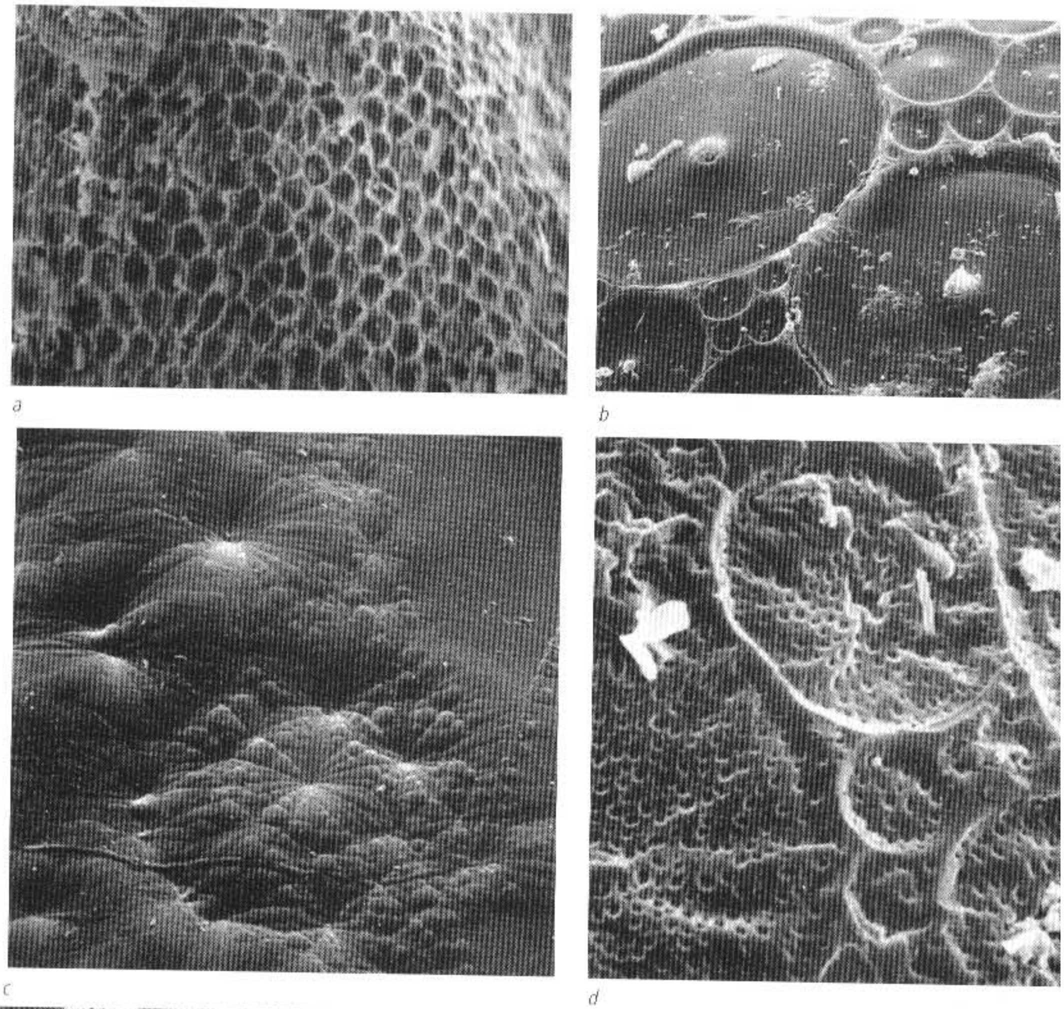


Fig. 2.41 The calcite skeleton of the sea urchin *Cidaris rugosa* appears to be a mineralized cast of a periodic minimal surface, the P-surface. (Photo: Hans-Udde Nissen, kindly supplied by Michele Emmer.)

Test-tube skeletons

As I indicated earlier, there can be practical value, as well as aesthetic pleasure, in patterned materials. There is now a whole battery of sophisticated techniques that materials scientists have at their disposal for imposing a pattern on a substance, and armed with electron and ion beams they can carve the most intricate circuitry into a silicon chip or etch semiconductor films into a microscopic mesh (Fig. 2.42). But these are extremely costly and labour-intensive methods, so the products do not come cheap. Nature, meanwhile, forms her patterns in very impure, messy chemical mixtures under the mildest of conditions and with profligate abundance. How much cheaper and easier it would be if we could learn a few tricks from her so as to effect the kind of patterning shown in Fig. 2.42 by throwing together a few chemical reagents in a bucket.

But if the delicate filigree of radiolarians and diatoms were the product of some complicated biological



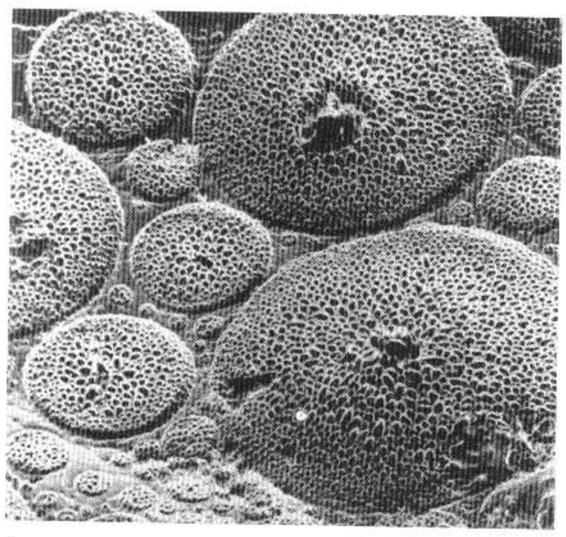


Fig. 2.44 An array of complex patterns formed 'in a beaker' frc mixture of organic surfactants and inorganic ions. (Photos: Scot and Geoffrey Ozin, University of Toronto.)

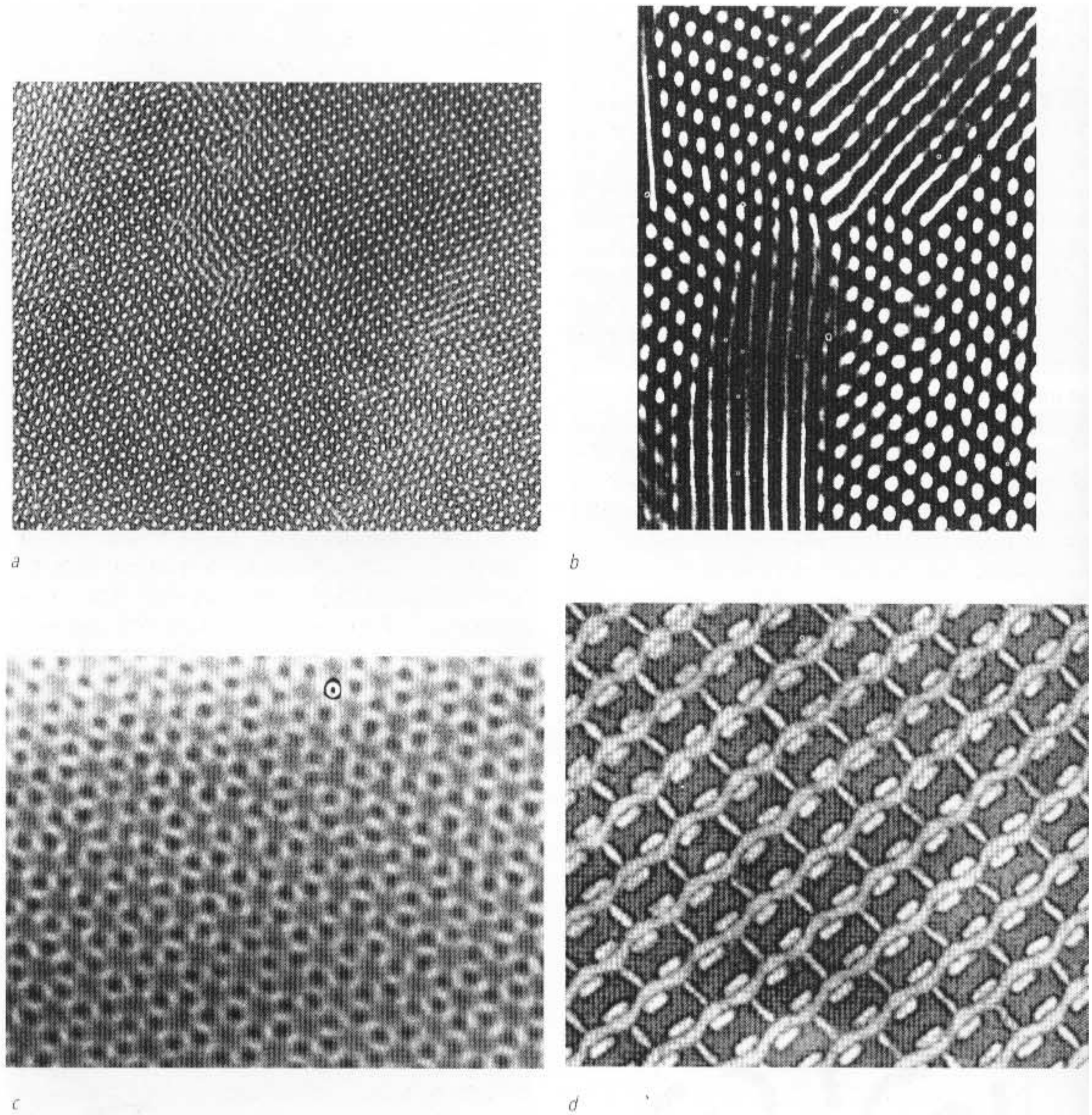


Fig. 2.46 The domains in block co-polymers can form ordered patterns: (*a*) a hexagonal array of spheres; (*b*) a hexagonal array of cylinders (here seen partly face-on); (*c*) the gyroid phase; and (*d*) a complex morphology seen in a three-block co-polymer. (Photos: Edwin Thomas, Massachusetts Institute of Technology.)

As we will see, complex patterns are very often born of such compromises. They emerge spontaneously from a delicate interplay of forces, and can often be altered in scale or in structure by a small shift in the balance of this interplay. They cannot be predicted by simply considering how the building blocks might be stacked together, but are *emergent* properties of the system as a whole. This is a theme that will recur throughout the book.

What *do* the bees know?

Was D'Arcy Thompson right, then, to see in the astonishing symmetry of a honeycomb nothing more

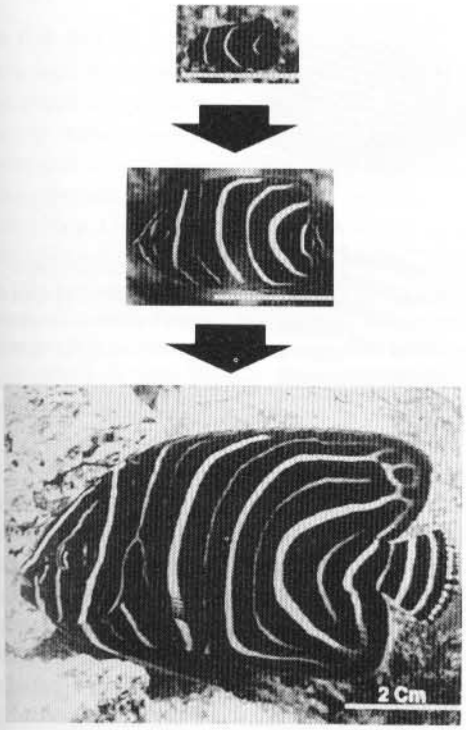


Fig. 4.22 As the angelfish grows, its stripes maintain the same width—so the body acquires more of them. This contrasts with the patterns on mammals such as the zebra or cheetah, where the patterns are laid down once for all and then expand like markings on a balloon. (Photo: Shigeru Kondo, Kyoto University.)

ing between stripes then reverts to that seen in the younger (2-cm) fish (Fig. 4.22). This process repeats again when the body grows to about 8 or 9 cm. In contrast, the pattern features on, say, a giraffe just get bigger, like a design on an inflating balloon.

This must mean that the angelfish's stripes are being actively sustained during the growth process—the reaction–diffusion process is *still going on*. One would expect that, if the fish were able to grow large enough (to the size of a football, say), the effect of scale evident in Jim Murray's work would kick in and the pattern would change *qualitatively*. But the fish stop growing much short of this point.

Kondo and Asai were able to reproduce this behaviour in a theoretical model of an activator–inhibitor process taking place in a growing array of cells. This is more compelling evidence for the Turing mechanism than simply showing that a process of the same sort can reproduce a stationary pattern on an animal pelt—the mechanism is able to reproduce the growth-induced expansion of the pattern too.

But the researchers went further still. They looked also at the angelfish *Pomacanthus imperator*, which has rather different body markings. The young fish have concentric stripes that increase in number as the fish grows, in much the same way as the stripes of *P. semicirculatus*. But when the fish become adult, the stripes reorganize themselves so that they run parallel to the head-to-tail axis of the fish. These stripes then multiply steadily in number as the fish continues to grow, so that their number is always proportional to body size, and the spacing between them is uniform. New stripes grow from branching points which are present in some of the stripes—the stripe 'unzips' along these branching points, splitting into two (Fig. 4.23*a*). The calculations of Kondo and Asai, using the same reaction–diffusion model as for *P. semicirculatus*, generated this behaviour exactly (Fig. 4.23*b*). Their model also mimicked the more complex behaviour of branching points located at the dorsal or ventral regions (near the top and bottom

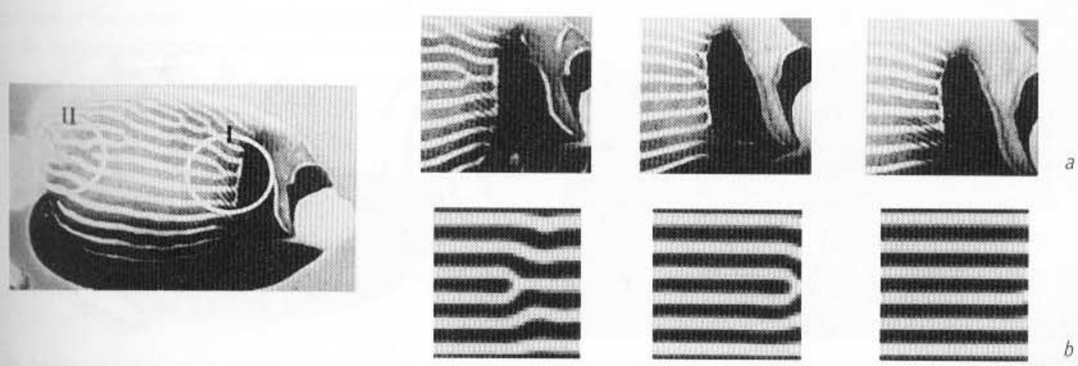


Fig. 4.23 The 'unzipping' of new stripes in *Pomacanthus imperator* (*a*; region I on the left) can be mimicked in a Turing-type model (*b*). (Photos: Shigeru Kondo.)