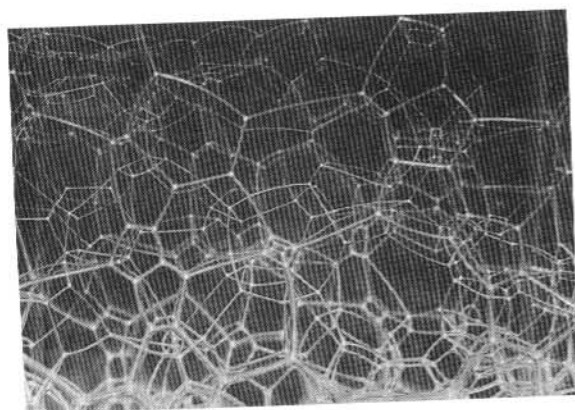


a



b

Fig. 2.8 A wet foam (a) consists of roughly spherical bubbles with water-laden walls. As the water drains away under gravity, the bubbles become more polyhedral and the result is a dry foam (b). (Photos: Burkhard Prause, University of Notre Dame, Indiana.)

larger ones. But as gravity sucks out the liquid from the walls and the cells become more like flat-sided polyhedra, the foam starts to take on some very particular geometric features. At first sight, it might seem to be a random mass of polyhedra of all shapes and sizes. At the end of the nineteenth century, however, a Belgian physicist named Joseph Antoine Ferdinand Plateau discerned some rules amongst the chaos.

First, the walls between cells are smooth, but not generally flat—they curve gently one way or another. This curvature indicates that the pressure of the gas inside the two adjacent cells is not equal: it is higher on the concave side of the wall. Smaller cells in a dry foam are the remnants of small bubbles, which (as Young and Laplace showed) have a higher internal pressure than

large bubbles; so where the two meet, the walls of the small cells bulge outwards (you can see this in Fig. 2.8b).

Where three walls meet, there is a junction in which the liquid film is slightly thicker than in the walls themselves (Fig. 2.9). Because the walls are necessarily curved at these junctions, the Young–Laplace relationship means that the pressure inside them must be lower than that in the flat walls; as a result, water is squeezed from the walls into the junction region. The consequence is that the junctions, called Plateau borders, contain most of the liquid in the foam.

Where three films meet in a Plateau border, the surface tensions in the films achieve a mechanical balance only if the walls meet at an angle of 120° (Fig. 2.9a). Equally, when four films meet, the angles at the junction would have to be 90° to achieve this balance of forces. But Plateau noticed a curious thing: he could find no fourfold junctions in his foams, nor any junctions of still greater numbers of walls. Three was the limit, and always with angles close to 120° .

The explanation for this requires a careful mathematical analysis of the various forces acting on the films, which I won't delve into. Suffice it to say that if four bubble walls *do* meet at a Plateau border, this turns out to be unstable and will rapidly rearrange to two threefold junctions (Fig. 2.9b). So here we have an explanation for why a two-dimensional packing of bubbles

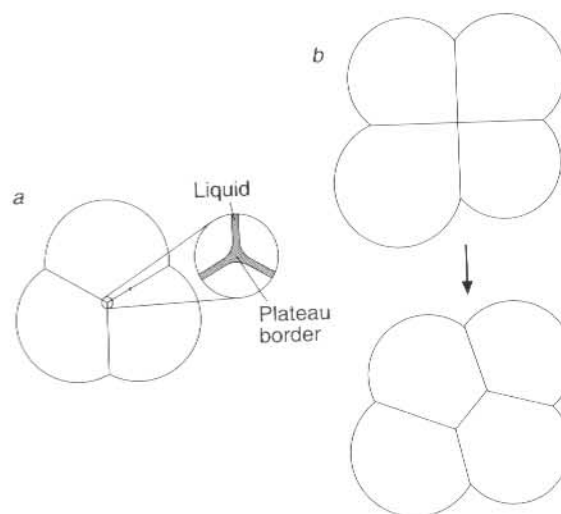


Fig. 2.9 Bubble walls meet at Plateau borders, where the walls are slightly thickened. Three walls will always meet at an angle of 120° at equilibrium (a). If, as a foam coarsens, four walls happen to come together at a junction, they will rapidly rearrange into two threefold junctions (b).



forms a foam of roughly hexagonal cells—only these satisfy the criterion that the walls always meet in threes with a 120° angle between them. Whether or not D'Arcy Thompson was right to ascribe the origin of the honeycomb's design to this effect, he was right about the way that bubbles pack.

But most foams are three-dimensional, and this means that Plateau borders along the edges of the polyhedral cells converge at their vertices. Here Plateau made another discovery: the number of Plateau borders that meet at a vertex seems always to be four—no more, no less. And they meet at an angle of about 109.5° , the 'tetrahedral angle': the four borders pointed to the vertices of a tetrahedron (Fig. 2.10). Again, this arrangement emerges from the requirements for mechanical stability of the cell walls. These geometrical rules govern the structures that all soap films will form when they meet (Fig. 2.11). They attest to an underlying regularity in the architecture of foams.

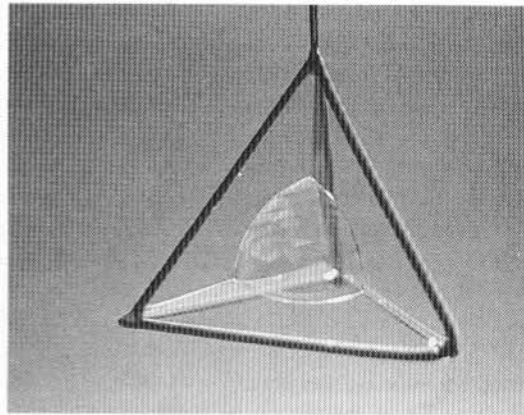
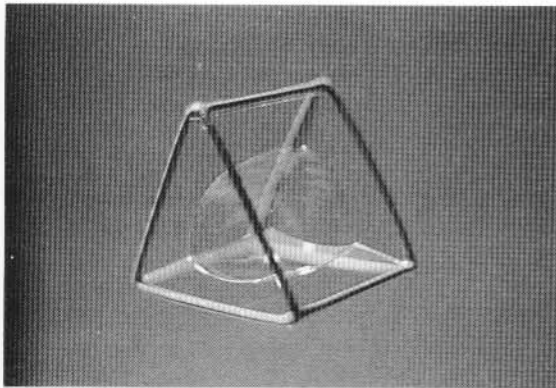
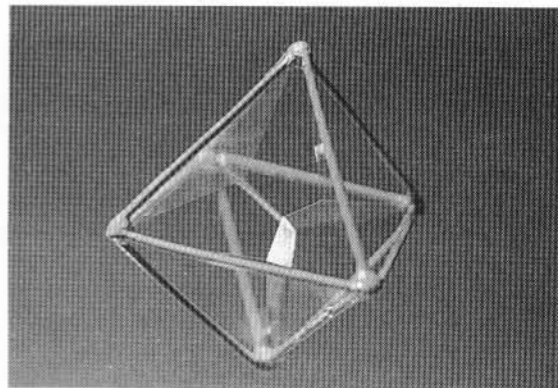


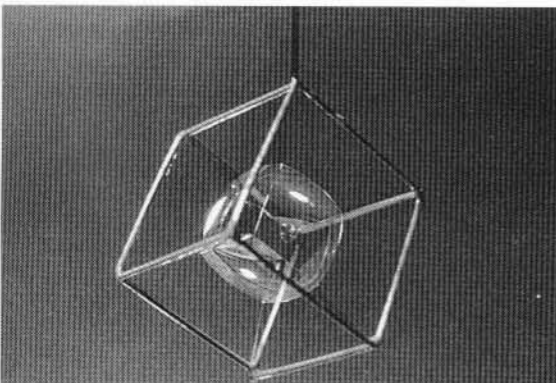
Fig. 2.10 Plateau borders converge at fourfold vertices, where they meet at the tetrahedral angle of about 109.5° . This is beautifully illustrated by soap films formed within a tetrahedral wire frame (see Appendix 1). (Photo: Michele Emmer, University of Rome 'La Sapienza'.)



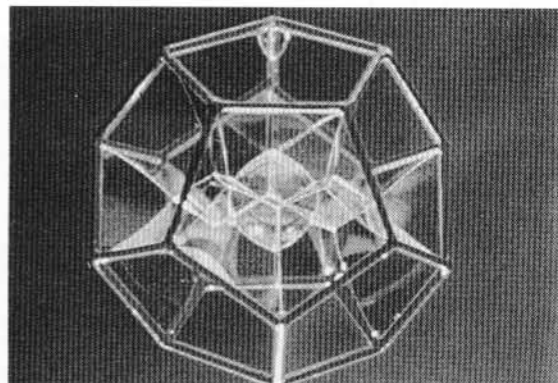
a



c



b



d

Fig. 2.11 The structures taken up by soap films and bubbles held within fixed boundaries are dictated by Plateau's rules. (Photos: Michele Emmer.)



Looked at more closely, however, Plateau's rules run into a problem. While we can understand how each arises in isolated packings of a few bubbles, we then have to ask whether it is in fact possible to fill up space with polyhedra that always conform to the rules. The simplest approach to the problem is to consider every cell to be identical in volume (as they are in a *monodisperse* foam), and to try to find a single polyhedral shape that can be packed together to give a network that obeys the rules governing borders and vertices. As well as satisfying these geometric criteria, the cells in this ideal three-dimensional foam should also minimize their total surface area. Is there a single, well-defined way to partition space so as to both satisfy Plateau's rules and provide the greatest economy in surface area? So far, no unique cellular packing of this sort has been identified.

This problem of cellular packing has a long history. In the eighteenth century, the English clergyman Stephen Hales took an inventive experimental approach, by compressing peas to see what shapes the spheres would take when flattened together. He claimed that the peas were pressed into 'pretty regular Dodecahedra', by which he apparently meant *rhombic* dodecahedra (Fig. 2.12a). These experiments were made widely known (though without attribution to Hales) by the French zoologist G.L.L. Buffon in 1753, and for a long time the rhombic dodecahedron was taken to be the best solution to the problem of economy. A rigorous mathematical proof was lacking, however, and in 1887

Lord Kelvin identified a cell shape that did better in terms of minimizing surface area: a 14-sided polyhedron (called a tetrakaidekahedron) with six square and eight hexagonal faces (Fig. 2.12b). This object, also known as a truncated octahedron, will pack together to fill space while coming close to satisfying Plateau's rules: at each vertex there are two 120° angles and one 90° angle, but Kelvin showed that only a slight curvature of the hexagonal faces is sufficient to adapt the vertices to the tetrahedral angle of 109.5° . Kelvin was not able to prove, however, that this was the most economical solution of all possible cellular packings, and no such proof has followed subsequently. Nevertheless, some mathematicians (including Hermann Weyl in his famous book *Symmetry*) have long suspected that Kelvin's solution cannot be bettered.

D'Arcy Thompson claimed that if a mass of clay pellets is compressed like Hales's peas, they will form shapes close to rhombic dodecahedra; but if they are first made wet, so that they can slide over one another, they show instead square and hexagonal facets like those of Kelvin's tetrakaidekahedron. So he was happy to conclude that soap bubbles of equal size, which can slide over one another, will form a froth with Kelvin's configuration. All the same, he cautioned that the solution to the packing problem depended in subtle ways on the conditions of packing: he described experiments by J.W. Marvin on compression of lead balls, which apparently formed rhombic dodecahedra if first stacked like a greengrocer's oranges in regular hexagonal layers, but irregular polyhedra with an average of 14 sides if poured into the vessel at random.

Moreover, the *regular* polyhedron (that is, one with identical faces) that comes closest to satisfying Plateau's rules is not the rhombic dodecahedron but the pentagonal dodecahedron, which has 12 pentagonal faces (Fig. 2.12c). This object doesn't stack to fill space exactly, and in addition the angles are slightly wrong— 116° between faces, 108° between vertices—but it will do the job with a little distortion. Another candidate for the cell shape in a monodisperse foam is an irregular 14-sided polyhedron called a beta-tetrakaidekahedron (Fig. 2.12d); but even this needs to be distorted to meet the rules.

So much for the models; what do the cells of real foams look like? The botanist Edwin Matzke conducted a detailed study of the shapes of monodisperse foams in 1946, and found that none of the ideal models provides, by itself, an accurate description of the cellular structure. For one thing, Matzke's foams were far from

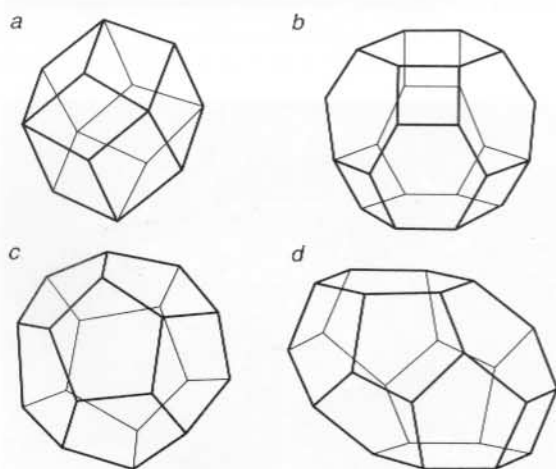


Fig. 2.12 Candidate cell shapes for a 'perfect' foam: (a) the rhombic dodecahedron; (b) the truncated octahedron promoted by Lord Kelvin; (c) the pentagonal dodecahedron; (d) the beta-tetrakaidekahedron.

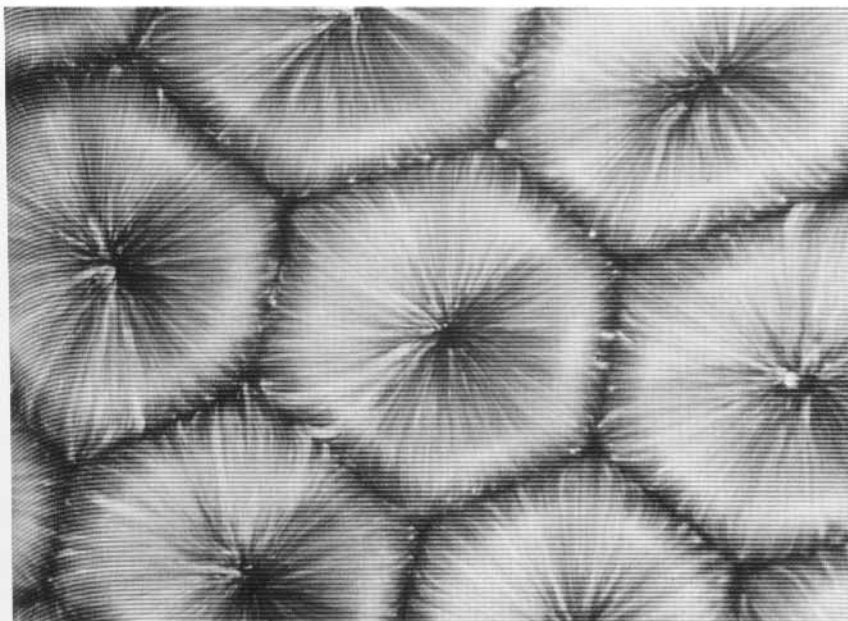


Plate 1 When a liquid is heated uniformly from below, it will spontaneously develop a pattern of hexagonal circulating cells. Here the cells are made visible by metal flakes suspended in the fluid. (Photo: Manuel Velarde, Universidad Complutense, Madrid.)

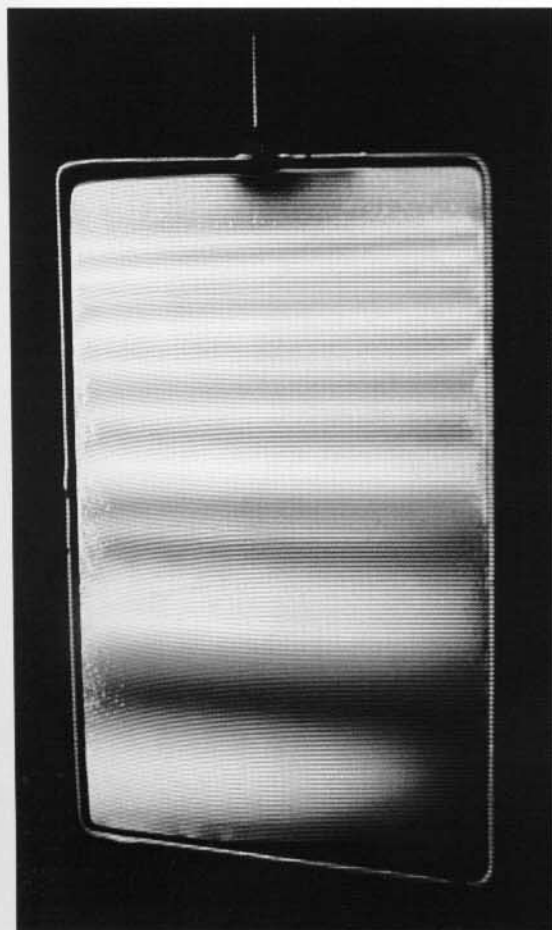


Plate 2 The rainbow colours of a soap film thinning under gravity. As the liquid in the film gets pulled downwards, the film's thickness varies from top to bottom. Interference between light reflected from the front and back of the film then selects different wavelengths of reflected light for different film thicknesses. The film turns silvery and then black before rupturing. (Photo: Michele Emmer, University of Rome 'La Sapienza'.)



regular—they contained cells of many different shapes, so that the structure could be described only in statistical terms. He observed that about 8% of the cells had roughly the shape of a pentagonal dodecahedron, although over half of the faces had five sides. Cells approximating Kelvin's truncated octahedra were even rarer—only 10% of the faces were four-sided, and Matzke found no cells resembling Kelvin's overall. Most of the cells tended instead to be rather like Marvin's squashed lead pellets, averaging about 14 sides each but with irregular shapes that might be best approximated by the beta-tetrakaidecahedron (Fig. 2.12*d*). Matzke's experiments suggested that the packing problem was purely academic, since perfectly regular foams are a Platonic ideal with no relevance to the real world.

But recently, physicists Dennis Weaire and Robert Phelan at Trinity College, Dublin, have questioned this conclusion. In 1993 they discovered a new type of cell shape for regular foams that finally deposed Kelvin's solution—after over a hundred years of supremacy—as the most economical solution to the packing problem. Their solution is less elegant than Kelvin's. Rather than a single cell type with faces that are regular polygons, the foam described by Weaire and Phelan has a repeat unit built up from eight cells, six of which have 14 faces and two of which have 12 (Fig. 2.13). The latter are pen-

tagonal dodecahedra, while the former have two hexagonal faces and 12 pentagons. But only the hexagonal faces are regular (with equal sides and angles); the pentagons in these cells have sides of differing lengths and corners of differing angles. All the same, this unit can be stacked together to give a regularly repeating foam structure whose surface area is about 0.3% less than that of a Kelvin-type structure of the same volume, while still maintaining Plateau's rules if the faces are almost imperceptibly curved.

Having identified this improved solution to the packing problem, Weaire and Phelan wanted to see if they could see it in real foams. So they decided to conduct a survey like Matzke's. But whereas Matzke had specified a highly complicated procedure for making monodisperse foams by adding bubbles one at a time, Weaire and Phelan found that they could produce these foams simply by using the 'drinking straw' technique of blowing bubbles underwater in a cylinder of liquid. They found first of all that the foams produced this way were not necessarily totally irregular and disordered, like Matzke's, but could contain regions in which regular cells were packed together. In parts of the foam close to the cylinder walls they often observed cells with square and hexagonal faces like those proposed by Kelvin (Fig. 2.14*a*); but these cell shapes seldom persisted beyond the first three or four layers. Within the bulk of the foam, meanwhile, they spotted regions where the cells had pentagonal and hexagonal faces, fitting together into structures very much like the one they had put forward as an improvement on Kelvin's (Fig. 2.14*b,c*). So it seems that after all, foams can be more geometrically precise—and more adept at the economical filling of space—than has long been believed.

Face to face

The problem of how to fill space with identical polyhedral cells, subject to a minimization principle for surface areas, is one that bees face too. The major part of the honeycomb problem is *two*-dimensional, because the cells are just prisms that are uniform along their length. What matters in this case is the cross-sectional shape of the cells, and the optimal solution in this regard is clear: hexagonal cells minimize the cross-sectional perimeter of the cell walls and so cost the bees less wax. But in the honeycomb, *two* such layers of cells are placed back to back, and the bees must then find the best way of marrying the two layers. The problem becomes three-dimensional, and so more complex, at the interface of the layers of cells.

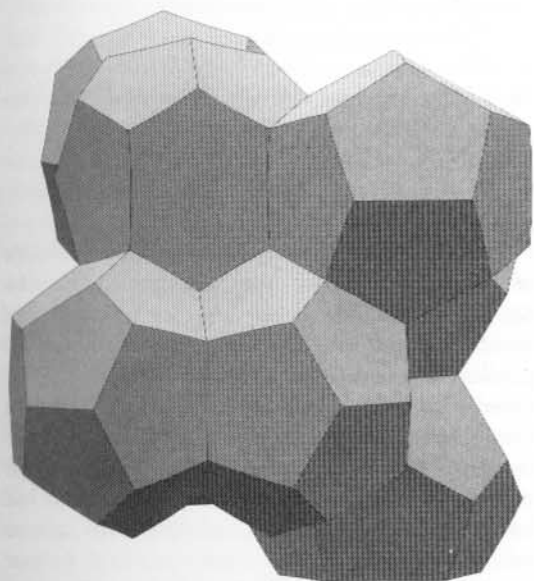
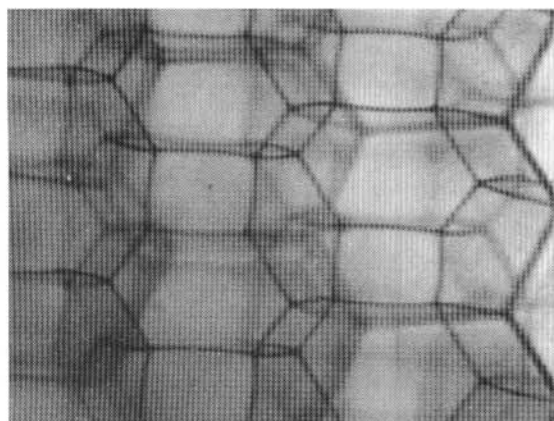
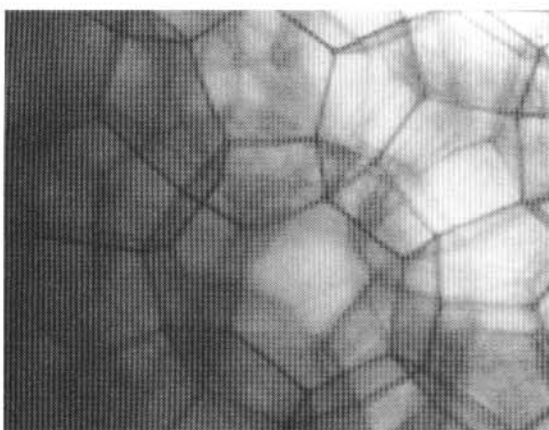


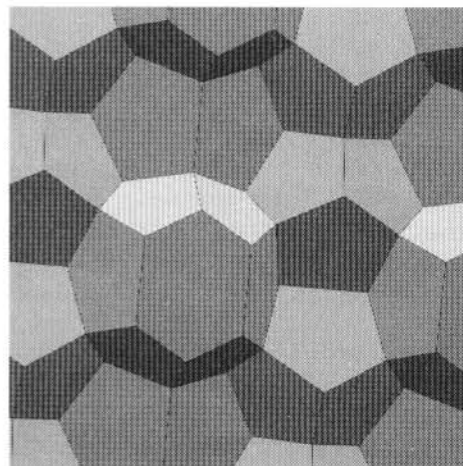
Fig. 2.13 A better foam? This cellular structure, proposed by Weaire and Phelan, has a slightly smaller surface area than that made of Kelvin's cells, for the same enclosed volume. The repeat unit consists of eight slightly irregular cells. (Image: Dennis Weaire and Robert Phelan, Trinity College, Dublin.)



a



b



c

Fig. 2.14 What does a real dry 'ideal' foam look like? At its boundaries are regions containing cells like Kelvin's (a), but deeper inside (b) are regions with cells like those of the 'minimal foam' of Weaire and Phelan (c). (Images: Dennis Weaire and Robert Phelan.)

This packing problem is entirely equivalent to that of filling space with polyhedral cells, except that it is confined to a single layer. In a real honeycomb each cell ends in three rhombic (four-sided) faces (Fig. 2.15a), which together constitute one fragment of the rhombic dodecahedron (Fig. 2.12a)—this relationship to the polyhedron seems to have been first identified by the sixteenth-century German astronomer Johannes Kepler. Back-to-back cells with these end caps marry perfectly, and in cross-section the interface has a zigzag structure (Fig. 2.15b). Is this the most economic solution to the problem?

Réaumur concluded in the eighteenth century that it was. He considered the case of two arrays of hexagonal cells meeting such that their end caps consist of three identical and equal-edged rhombuses, and asked the

Swiss mathematician Samuel Koenig to find the shape of the rhombuses that minimized the surface area. Koenig showed that the angles of each rhombic face should be about 109.5° and 70.5° , which are those in the regular rhombic dodecahedron—and also those observed in real honeycombs. It was this finding that led the secretary of the French Academy, Fontenelle, to issue the pronouncement on the divine guidance of bees quoted on page 17. To reach his solution, Koenig had had to employ the methods of differential calculus introduced less than half-a-century previously by Isaac Newton and Gottfried Wilhelm Leibniz, and it was too much for Fontenelle to suppose that the bees could possess this knowledge that surpassed 'the forces of common geometry'—for that would surely mean that 'in the end these Bees would know too much, and their

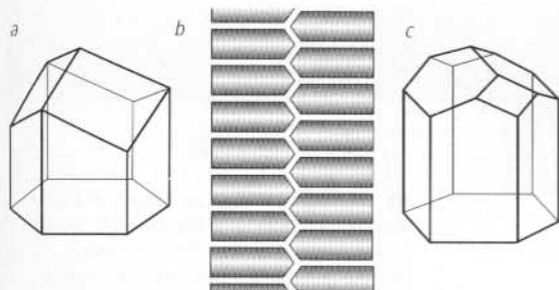


Fig. 2.15 The ends of a honeycomb's cells are fragments of rhombic dodecahedra, made up of three rhombic faces (a). The two layers of cells with these end caps marry up with a zigzag cross-section (b). Is this the minimal solution? A smaller surface area is obtained for end caps that are fragments of Kelvin's truncated octahedra (c).

exceeding glory would be their own ruin'. Evidently the geometric excellence was that of God, not of mere creatures.

But in posing the problem, Réaumur had imposed constraints (the requirement of three identical rhombuses) that left doubt as to whether the bees have truly found the optimal answer. In 1964 the Hungarian mathematician L. Fejes Tóth pondered on the economy of the honeycomb in a lecture entitled 'What the bees know and what they do not know'. He showed that a better solution exists in which the cells' end caps are more elaborate—a combination of squares and hexagons (Fig. 2.15c). This structure represents a total saving of a tiny fraction of a percent of each cell's surface area. Just as the rhombic cap is related to the rhombic dodecahedron, so Tóth's cell is closely related to the truncated octahedron (Fig. 2.12b) that Kelvin showed to be more economical in three dimensions. Tóth emphasized that, while his was mathematically a superior solution, there was no guarantee that it was biologically better—for the bees might have to expend more effort in making the more elaborate end-caps.

Weaire and Phelan have used their foam-blowing technique to put Tóth's idea to an experimental test. They looked at the cell structures in a thin foam—two layers of bubbles—constrained between glass plates. The bubbles adopt hexagonal faces at the interface with the glass, so that the foam is a precise analogue of the honeycomb. They found that the interface between the two layers of bubbles does adopt Tóth's structure (Fig. 2.16a), which can be identified by the distinctive pattern made by the junctions of bubbles in projection. But if Weaire and Phelan thickened the bubble walls by adding more liquid (creating a wet foam), they found

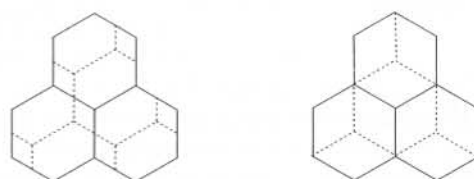
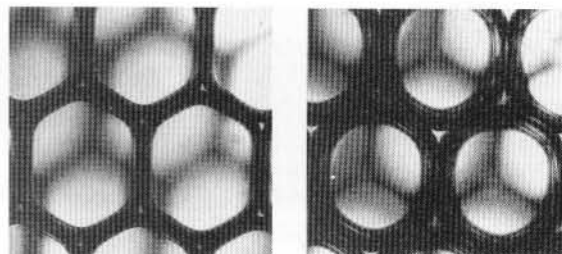


Fig. 2.16 Tóth's structures can be seen at the interface of a double layer of hexagonal bubbles (a). But if the bubbles contain more liquid in their walls, the faces at the interface change to rhombuses (b), giving a junction like that in real honeycombs (Fig. 2.15a, b). (Photos: Dennis Weaire and Robert Phelan.)

something unexpected: as the bubbles become more rounded, there is a point at which the interface suddenly switches to the three-rhombus configuration found in the real honeycomb (Fig. 2.16b). The thickening of the walls and curving of the bubble sides apparently changes the balance in surface energies so that this structure becomes more stable instead. So in thicker-walled honeycombs, maybe the bees *do* have the best solution. Do they know more than we thought? I return to this question at the end of the chapter.

Curved spaces

Cells, starfish and doughnuts

Soap bubbles and foams do not last for ever, and I suppose that is part of their appeal: fragile beauty, gone in a moment. The collapse of foams is brought about partly by the drainage of the films, under the influence of gravity and capillary forces, until they become too thin to resist the slightest disturbance—a vibration or a breath of air. But in their passing, soap films can treat us to a wonderful display. Held vertically on a wire frame, a thinning soap film becomes striated with bands of rainbow colours that pass from top to bottom (Plate 2). Finally the top becomes silvery and then black; and the blackness, like a premonition of the film's demise,

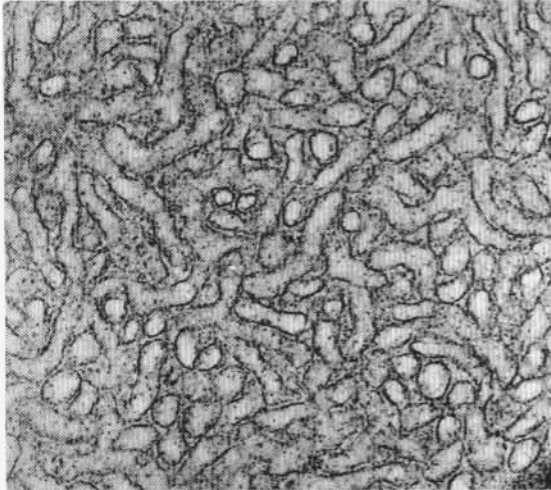


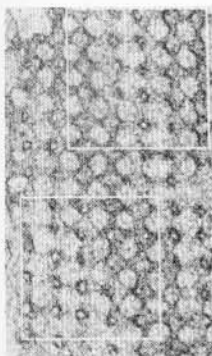
Fig. 2.31 The cell's smooth endoplasmic reticulum is a disordered 'sponge' of natural membranes. (Photo: Don Fawcett.)

There most certainly are! Membranes with regular channel structures akin to periodic minimal surfaces have now been identified in the cells of countless organisms ranging from bacteria to plants to rats. Kåre Larssen, Tomas Landh and colleagues at Lund University in Sweden have shown that the biological literature is replete with images of ordered membrane networks (Fig. 2.32), many of them apparently corresponding to periodic minimal surfaces or surfaces of constant mean curvature. They had not previously been recognized as such, says Landh, because cell biologists,

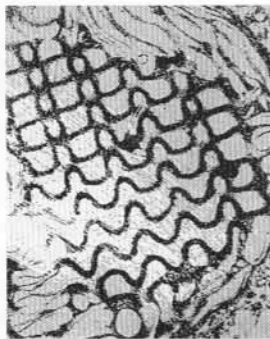
unfamiliar with these mathematical abstractions, had been unable to interpret what they saw.

The first pictures of such structures were presented in 1965 by Brian Gunning, who observed them in electron microscope images of plant cells. These are much like the pictures that one can see through a light microscope—lighter where there is less dense matter and darker where the density is greater—but because the images are formed by the scattering of electrons rather than light, they have a higher resolution: smaller features can be seen. (The limit on the size of the objects a microscope can resolve is set by the wavelength of the imaging beam, and a beam of electrons typically has a shorter wavelength than visible light.) The complication, however, is that these electron micrographs show projections—two-dimensional 'shadows' of the three-dimensional structure. This can make it very hard to decide exactly what kind of three-dimensional pattern is being imaged, and in general researchers have to rely on comparisons between the real images and simulated images calculated by assuming a particular 3D structure (Fig. 2.33).

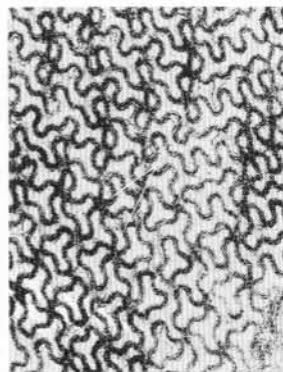
Gunning saw a hexagonal pattern in the micrographs of leaf cells—the projected image of a regular network formed from the biological membranes. In 1975 he and botanist Martin Steer proposed that these networks were periodic minimal surfaces. In 1980 Larssen and his co-workers at Lund suggested that some of Gunning's images corresponded to the D-surface (Plate 3a). Soon other structures began to come to light in the organelles—the functional compartments—of many other cells. They are particularly common in the endoplasmic reticulum, but are also found in the membranes



a



b



c

Fig. 2.32 Periodic membrane structures are common in living cells. Many of these appear to be related to periodic minimal surfaces: (a) the D-surface in leaf membranes; (b) the P-surface in algae; (c) the G-surface in lamprey epithelial cells. (Photos: a, from Gunning (1965), *Protoplasma* **60**, 111; b from McLean & Pessoney (1970), *J. Cell Biology* **45**, 522. All images kindly provided by Tomas Landh, Lund University.)