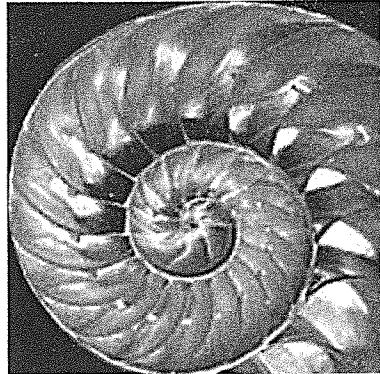


PATTERNS

The waves of the sea, the little ripples on the shore, the sweeping curve of the sandy bay between the headlands, the outline of the hills, the shape of the clouds, all these are so many riddles of form, so many problems of morphology, and all of them the physicist can more or less easily read and adequately solve.

D'Arcy Wentworth Thompson
On Growth and Form



There was always something a little different about meteorite ALH84001, found in 1984 on the icy Allan Hills of Antarctica. For one thing, it came from Mars—like only 11 other meteorites found around the world. But unlike these others, ALH84001 was *old*—and I mean four-and-a-half billion years old. The rock was formed when the Red Planet was newly born. But the most extraordinary aspect of this little lump of Mars did not emerge until August 1996, when scientists from NASA announced that it might contain signs of fossil life from our cosmic neighbour.

Maybe my years at *Nature* magazine have exposed me to too many amazing 'discoveries' that vanish like morning mist under close scrutiny; but I felt in my bones that this claim would not stand the test of time. If I'm wrong (and I rather hope I am), this is one of the most significant discoveries of the twentieth century. But although the jury is still out while scientists clamour for more pieces of the meteorite to carry out exacting tests, already there are signs that this evidence for ancient life on Mars is on shaky ground.

One of the lines of argument particularly caught my attention. Within the Martian rock the NASA team found microscopic wormlike features about a tenth of a micrometre in width, which they suggested might be the fossilized remains of bacteria (Fig. 1.1). What leapt to my mind was a book called *Earth's Earliest Biosphere*, in which Californian geologist William Schopf lists and depicts countless examples of curious, bacteria-like structures in ancient rocks from Earth's early history. Schopf explains that, while some of these are indeed microfossils of primitive bacteria dating back to around a billion years after the Earth was formed, many others are not fossils at all, but most probably structures formed in the rocks by purely geological processes.

Prospectors for early life on Earth are in constant danger of being fooled by these mineral structures, which in some cases look barely distinguishable from well-established microfossils (Fig. 1.2). There is a recognized class of objects called 'dubiofossils', which are microscopic rock structures whose origin one cannot

unambiguously ascribe either to organic or inorganic causes. I should say that the NASA scientists were familiar with these pitfalls, and were also uncomfortably aware that their putative Martian fossils were much smaller than any known from Earth. But they felt that the several other suggestive chemical characteristics of meteorite ALH84001 added weight to the idea that the worm-like structures were indeed the mineralized casts of primitive organisms from Mars.

You might think that it should be an easy matter to distinguish a fossilized remnant of a living organism from some rock feature formed by physical forces alone. Surely we can, at even a brief glance, tell a crystal from a living creature, an insect from a rock?

Yet what is it that encourages us to make these distinctions, based on superficial features alone? I suspect that most of us at some level identify a kind of characteristic form that we associate with living things; but it is hard to put that into words. Living organisms come in all shapes and sizes—a tree, a rabbit, a spider—but there is something purposeful about these forms. They are complex (and I shall shortly have to be a little more

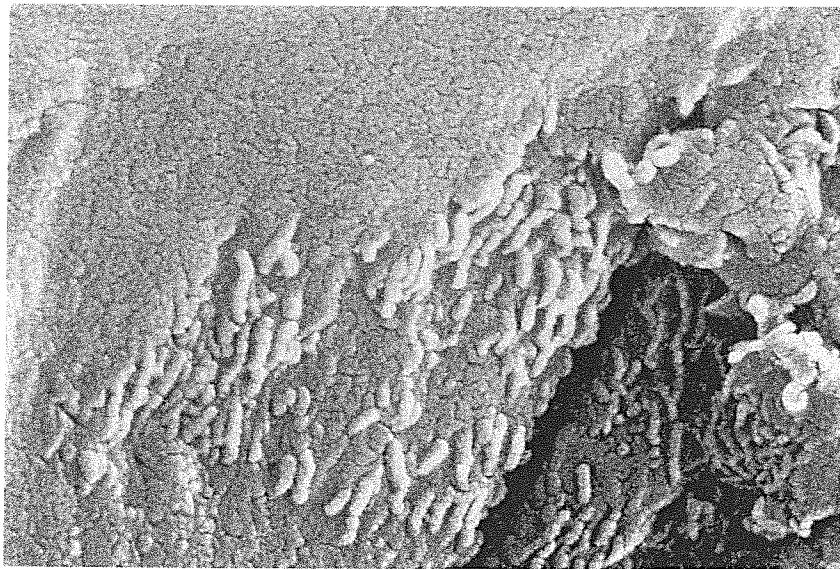


Fig. 1.1 These microscopic structures found in a Martian meteorite have been presented as evidence for ancient bacterial life on Mars. Are they the fossilized remnants of tiny worm-like organisms? (Photo: NASA.)

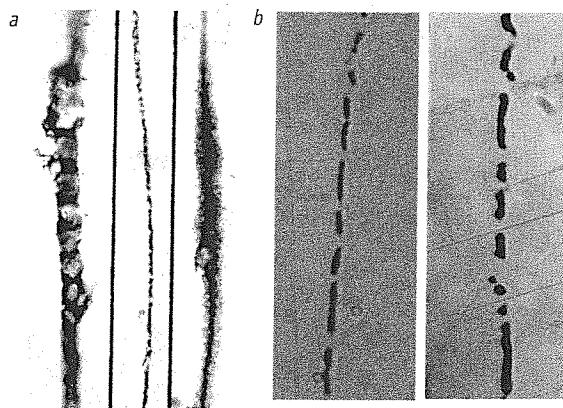


Fig. 1.2 How do you tell a fossil from a rock? The formations shown here have all been identified in ancient rocks; but whereas those in (a) are probably genuine fossilized bacteria, several billions of years old, it is possible that those in (b) were formed by purely geological processes. (Photos: from W. Schopf (ed.) (1991). *Earth's Earliest Biosphere*. Reprinted with permission of Princeton University Press.)

precise in using this word), but not random. They have a kind of regularity—evident, for instance, in the bilateral symmetry of our bodies or in the branching pattern of a tree—but it is not the geometric regularity of crystals. Somehow it seems natural, when we see forms like those in Fig. 1.1, to associate them with the

subtle and delicate forces of life, not with the coldly geometrical exigencies of physics.

If there is one thing I hope to do in this book, it is to shake up these assumptions. I wish to show in particular that pattern and organized complexity of form need not arise from something as *complicated* as life, but can be created by simple physical laws. This idea of complexity from simplicity has become almost a new scientific paradigm in recent years, and most probably a cliché too. Yet I hope here to tie it down, to show that it is not a recondite solution to all of life’s mysteries, nor a result of a newly acquired facility for tricky computer-modelling, nor even a particularly new discovery—but a theme that has featured in scientific enquiry for centuries. Some of the complex patterns that I shall consider in this book pose questions that are truly ancient: from where come the stripes of a tiger, the procession of ‘mare’s tail’ clouds, the undulations of sand dunes, the vortex of a whirlpool, the shapes and decorative adornments of sea shells?

Imposters

Let me delve further into our preconceptions about form and pattern. If you saw through the microscope mineral formations like those in Fig. 1.3a, would you suspect that these are the shells or skeletons of some tiny creatures? That would be an understandable assump-

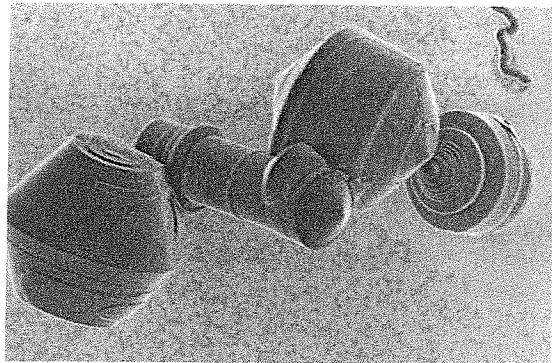
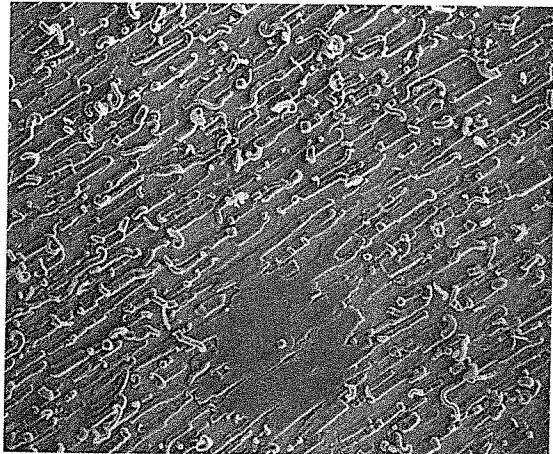
*a**b*

Fig. 1.3 (a) Are these complex, patterned mineral structures the shells or skeletons of tiny organisms? On the contrary, they are the product of a purely synthetic chemical process carried out in the laboratory. (b) A similar chemical process generates these surface patterns, which bear some (coincidental) resemblance to those in Fig. 1.1. (Photos: Geoffrey Ozin, University of Toronto.)

tion, yet they are the products of a purely chemical process involving the precipitation of silica from a soluble salt. Much the same chemical brew can produce the surface patterns in Fig. 1.3*b*, strikingly reminiscent in both shape and scale of the putative Martian fossils in Fig. 1.1! What on earth sculpts these mineral bodies into such odd and apparently ‘organic’ forms?

A particularly striking cautionary tale of this association between life and complex form—and one that reverberates through the story of the Martian meteorite—concerns the rock formations known as stromatolites that are found in ancient reef environments

around the world. Ever since these curious, spongy structures were discovered in the nineteenth century, their origin has been disputed. The prevailing interpretation is that they represent the fossil remains of mat-like structures created by marine microorganisms such as cyanobacteria, which are amongst the oldest known forms of life on Earth. Fossil microbes *have* been found in some stromatolites, but the argument for their biological origin finds its most crucial evidence in the similarity in form between ancient stromatolites and modern analogues that are demonstrably still being

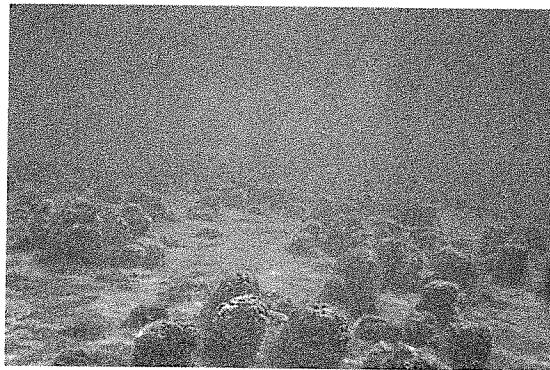
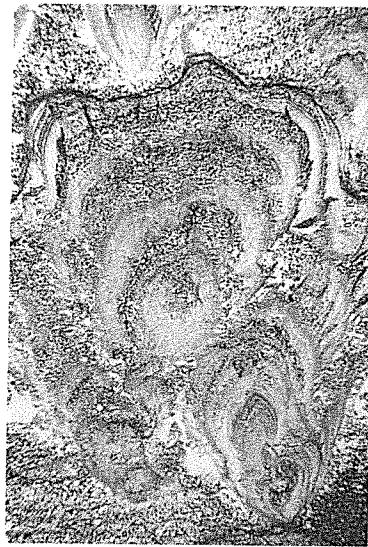
*a**b*

Fig. 1.4 (a) Modern-day stromatolites in Shark Bay, Western Australia. (b) The complex, laminated structure of a 2.7-billion-year-old stromatolite from Western Australia. The image shows an area of 3 × 4 cm. (Photos: Malcolm Walter, Macquarie University, Sydney.)



constructed from cyanobacterial and algal mats (Fig. 1.4a). If this association holds, stromatolites provide some of the oldest evidence for life on Earth, since they have been dated back to three-and-a-half billion years ago. Researchers have even proposed that searches for life on Mars itself should include the option of looking for stromatolite-like features around the dried-up lakes and springs of the Red Planet.

But in 1996 John Grotzinger and Daniel Rothman from the Massachusetts Institute of Technology showed that a comparison based on form alone cannot provide unambiguous evidence for the handiwork of biology. They demonstrated that the characteristic features of the irregular layers of a typical stromatolite (Fig. 1.4b), whose bumps and protrusions look for all the world like the product of biological growth, can be generated by simple physical processes of sedimentation and precipitation of minerals from the overlying water. This does not prove that stromatolites *are* purely geological structures (and it is virtually certain that at least some are not), but it shows that arguments based on form alone are not sufficient to rule out that possibility.

We can play this game the other way around. What are the objects shown in Fig. 1.5—living organisms or crystals? Their geometric regularity suggests the latter, but these are viruses, and all too dangerously alive. Complex form may not require an organic origin, but similarly geometric form does not exclude it. There are, in other words, forces guiding appearances that run deeper than those that govern life.

Look—no hands

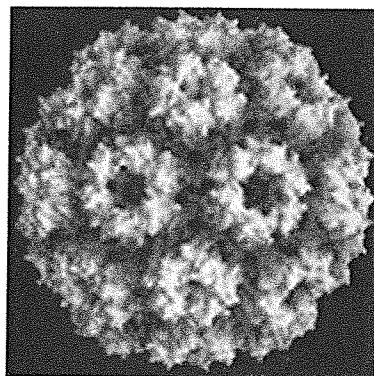
Our prejudice says otherwise. The most striking examples of complex pattern and form that we encounter tend to be the products of human hands and minds—shaped with intelligence and purpose, constructed by

design. The convolutions of a traditional patchwork fabric, the intertwining knots of a Celtic symbol, the horizon-spanning stepped terraces of Asian rice fields, the delicate traceries of microelectronic circuitry (Fig. 1.6)—all bear the mark of their human makers. The subconscious message that we take away from all this artifice is that patterning the world—shaping it into the forms of our needs and our dreams—is hard work. It requires a dedication of effort and a skill at manipulation. Each piece of the picture must be painstakingly put into place, whether by us or by nature. This, we have come to believe, is the way to create any complex form.

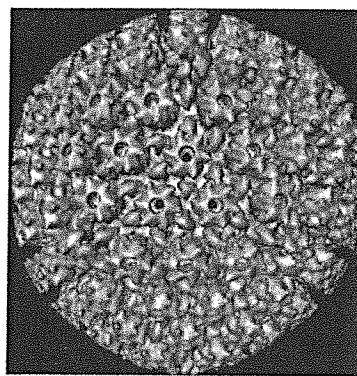
So when they found complexity in nature, it is scarcely surprising that many theologians throughout time have refused to see anything other than the signature of divine guidance. From the action of nature's most basic physical laws, on the other hand, such as Newton's inverse-square law of gravity, we have learnt to expect nothing but the geometric sterility of a planet's elliptical orbit around the Sun.

Would it not be extraordinary, however, if these laws could by themselves contrive to generate rich and beautiful patterns? If we could decorate a table cloth by using dyes that spontaneously segregate into a multicoloured design? Or to scatter a hillside with topsoil and watch it arrange itself into terraces ready to receive water and seed? But experience teaches us that this is not the way things go. On the contrary, dyes mix, don't they? Soil gets distributed randomly by the wind and rain, right?

The astonishing thing is that sometimes apparent reversals *do* happen. Fluids unmix of their own accord; landscapes become sculpted by the elements into regular patterns. Through such processes, nature's tapestry embroiders its own pattern. And by studying these strange and counter-intuitive processes, we discover that some of nature's patterns recur again and again in



a



b

Fig. 1.5 These geometric, ordered forms are in fact living organisms—viruses. (a) The cowpea chlorotic mottle virus; (b) the herpesvirus. (Images: (a) Jean-Yves Sgro, University of Wisconsin; (b) Hong Zhou, University of Texas at Houston.)

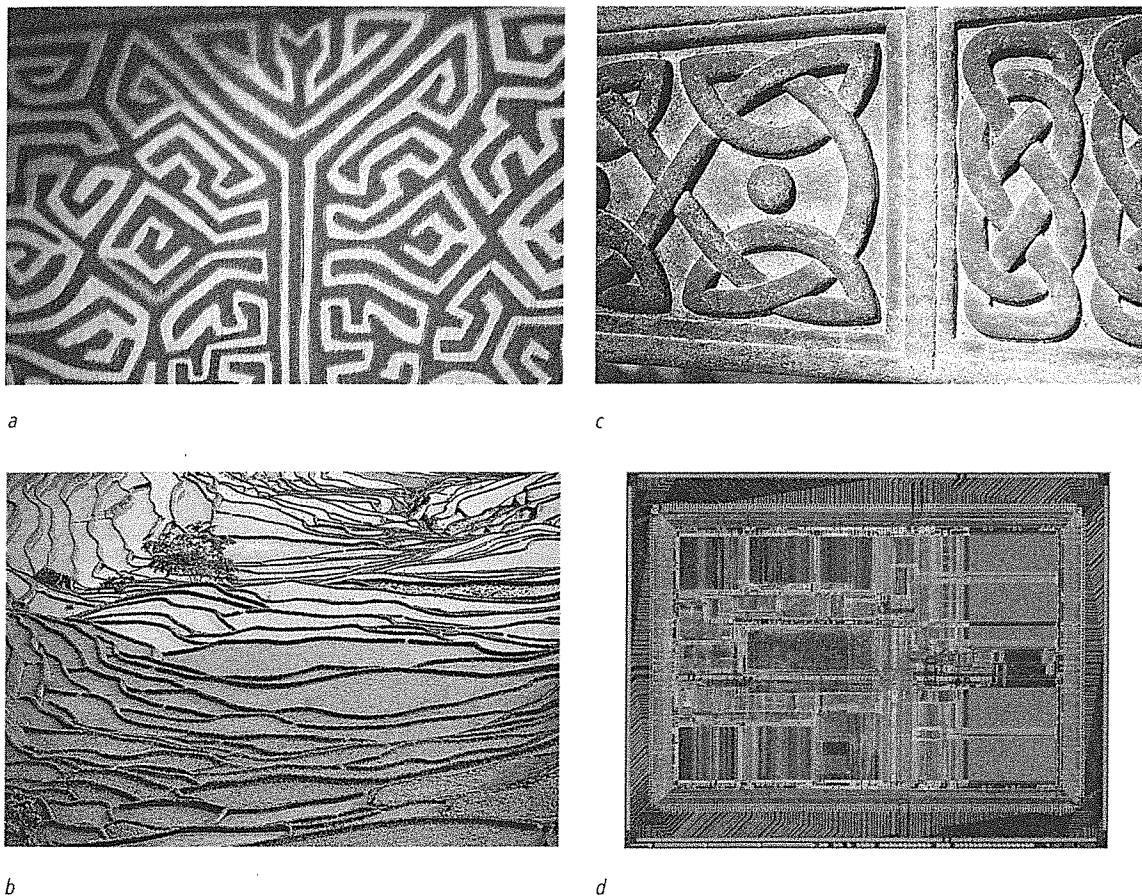


Fig. 1.6 Most of the complex patterns that we create are the products of painstaking labour: (a) a Kuna *mola* tapestry from Panama; (b) paddy fields in China; (c) Celtic design on a stone cross; (d) circuitry on a microprocessor chip. (Photos: (b) Getty Images; (d) Michael W. Davidson and the Florida State University.)

situations that appear to have nothing in common with one another. You can't avoid concluding, once you begin to examine this tapestry, that much of it is woven from a blueprint of archetypes, that there are themes to be discerned within the colourful fabric. Nature's artistry may be spontaneous, but it is not arbitrary.

Form and life

Biologists are used to the idea that form follows function. By this I mean that the shape and structure of a biological entity—a protein molecule, a limb, an organism, perhaps even a colony—is that which best equips the organism for survival. (In today's gene-centred view of biology, we should instead strictly say that it is the survival of the gene that is paramount, the organism

being merely a convenient vehicle for this.) This is the Darwinian paradigm: form is selected from a palette of possibilities, and by selected I mean favoured by *natural selection*. A form that gives the organism an evolutionary advantage tends to stick.

This is a simple idea, but phenomenally powerful. The objection that it would take an unreasonably long time to find the best form from the range of alternatives—a favourite argument for evolutionary sceptics—crumbles beneath the extraordinary and demonstrable efficiency of natural selection. We can watch the process take place in a matter of days for generations of bacteria bred in culture. In 1994, Swedish researchers performed computer experiments showing that even a biological device as sophisticated as an eye will evolve from a flat sandwich of photosensitive cells



in a matter of around 400 000 generations—perhaps half-a-million years, a blink in geological terms—if one makes conservative assumptions about such factors as the rate of mutation between each generation. Even getting life started in the first place, from a brew of simple organic chemicals on the young Earth, seems to have been astonishingly easy: it may have taken less than 200 million years from the time that the planet first had a solid surface, and would presumably have involved competition and consequent selection amongst generations of replicating molecules and small molecular assemblies.

But as an explanation for natural form, natural selection is not entirely satisfying. Not because it is wrong, but because it says nothing about mechanism. In science, there are several different *kinds* of answer to many questions. It is like asking how a car gets from London to Edinburgh. One answer might be ‘Because I got in, switched on the engine, and drove’. That is not so much an explanation as a narrative, and natural selection is a bit like that—a narrative of evolution. An engineer might offer a different scenario: the car got to Edinburgh because the chemical energy of the petrol was converted to kinetic energy of the vehicle (not to men-

tion a fair amount of heat and acoustic energy). This too is a correct answer, but it will be a bit abstract and vague for some tastes. Why did the car’s wheels go round? Because they were driven by a crankshaft from the engine... and before long you are into a mechanical account of the internal combustion engine.

Some biologists want to know about the internal combustion engine of biological form. They will accept that the form is one that conveys evolutionary success, that a fish shaped like a giraffe wouldn’t exactly have the edge on its competitors. But this form has nonetheless to be put together from a single cell. What are the mechanical ins and outs of that process?

From a naive evolutionary perspective, anything seems possible. You assume that nature has at its disposal an infinite palette, and that it dabbles at random with the choices, occasionally hitting on a winning formula and then building mostly minor variations on that theme: for fish, the torpedo-body-and-fins theme, for land predators the four-legs-and-muscle idea. To judge from the astonishing diversity of form apparent in fossils from the Cambrian period (Fig. 1.7; see also Stephen Jay Gould’s book *Wonderful Life*)—a diversity far exceeding anything we find in today’s organisms—you might imagine that this is precisely what happens. But is the palette truly infinite? Once you start to ask the ‘how?’ of mechanism, you are up against the rules of chemistry, physics and mechanics, and the question becomes not just ‘is the form successful?’ but ‘is it physically possible?’

Questions of this sort were what prompted the Scottish zoologist D’Arcy Wentworth Thompson in 1917 to write a beautiful book whose influence is still felt today. In *On Growth and Form*, Thompson gave an engineer’s answer to the Darwinism that was rushing like a deluge through the biology of his time. Still in its first flush, Darwin’s theory was propounded as the answer to every question that someone in Thompson’s community might want to ask. The shape of a goat’s horn, of a jellyfish’s protoplasmic body, of a sea shell—all have the form they do because natural selection has sculpted them that way.

D’Arcy Thompson saw such ideas as an affront to one of science’s guiding principles: economy of hypotheses, exemplified by the approach to problem solving expounded by the fourteenth-century philosopher William of Ockham and now known as Ockham’s (or Occam’s) razor. Put simply, this approach demands that we set aside complicated explanations for things when a simpler one will do. The principle is not much fun—there would be no UFOs, no paranormal phenomena, if

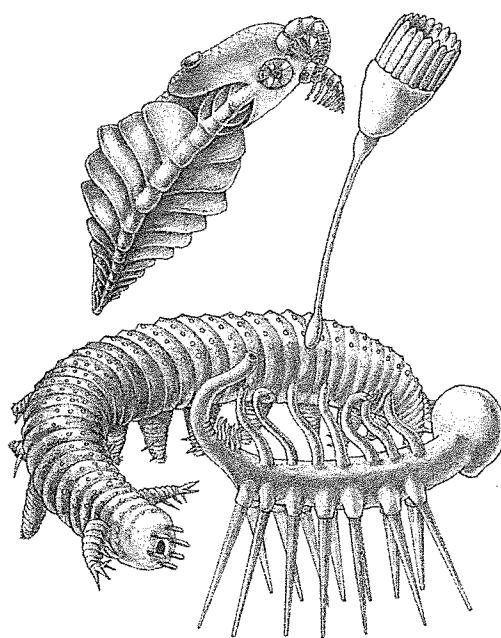


Fig. 1.7 The Cambrian period was a time of tremendous experimentation in nature’s body plans. Here are just a few of the bizarre creatures reconstructed from remains found in the Burgess shale. Clockwise from top left: *Anomalocaris*, *Aysheaia*, *Hallucigenia* and *Dinomischus*. (Drawn by the author, after Marianne Collins.)



we had all learnt to observe it—but it prevents the proliferation of unnecessary ideas.

What, suggested Thompson, could be more unnecessary than invoking millions of years of selective fine tuning to explain the shape of a horn or a shell when one could propose a very simple growth law, based on *proximate physical causes*, to account for it? The sabre-like sweep of an ibex horn does not have to be selected from a gallery of bizarre and ornate alternative horn shapes: we can merely assume that the horn grows at a progressively slower rate from one side of the circumference to the other, and hey presto—you have an arc.

There is no inconsistency here with the Darwinian scheme of things, within which it is quite possible for such a growth law to arise. But Thompson's point was that it need not have been *selected*—it was inevitable. Either the horn grew at the same rate all around the circumference, in which case it was straight, or there was this imbalance from one side to the other, giving a smooth curve. It just did not make sense to invoke other shapes: nature's palette contains just these two. Even the more elaborate spiral form of a ram's horn need be only the manifestation of a stronger degree of imbalance, causing the horn's tip to curve through several complete revolutions.

In D'Arcy Thompson's view, some biological forms, the shapes of amoeba say, can no more be regarded as '*selected for*' than can the spherical form of a water droplet; rather, they are dictated by physical and chemical forces. To support this assertion he evinced many organisms whose shapes could be explained as a more or less inevitable corollary of the forces at work. What was the point, he asked, in accounting for the shape of a bone in evolutionary terms (which 'explained' nothing) when it could be rationalized through the same engineering principles that engineers use to design bridges? Skeletons are then seen not as arbitrary structures moulded this way and that by natural selection, but as constructions that must satisfy engineering requirements. The same is true of trees, and of all living forms whose stability is dominated by gravity. When small size reduces the influence of gravity, surface tension takes over and a new set of forms can result.

Despite, or perhaps because of, Thompson's erudition and facility with other disciplines (he was also a professor of Ancient Greek), *On Growth and Form* has a quixotic air. It sometimes veers in spirit towards the ideas of the Frenchman Jean Baptiste Lamarck, who argued before Darwin that evolution was a response to the environment, in which adaptation is not the result

of random mutations but is guided along a preordained path by the environmental forces to which organisms are subject. Today this idea is biological heresy.

On Growth and Form came close to heresy too, and Thompson was conscious of it. 'Where it undoubtedly runs counter to conventional Darwinism', he said when submitting the manuscript, 'I do not rub this in, but leave the reader to draw the obvious morals for himself.' And so they did: the English biologist Sir Peter Medawar called the book 'Beyond comparison the finest work of literature in all the annals of science that have been recorded in the English tongue'. Without a doubt, it is beautifully written and deeply scholarly. But to what extent was Thompson right?

The black box of genetics

In its most basic form, D'Arcy Thompson's thesis was that biology cannot afford to neglect physics, in particular that branch of it that deals with the mechanics of matter. (He was far less concerned with chemistry, the other cornerstone of the physical sciences, but that seems to have been because he did not consider it sufficiently mathematical. Today there is much in the field of chemistry that would have served Thompson well.) His complaint was against the dogma of selective forces as the all-pervasive answer to questions in biology. For him this did not answer questions about causes; it merely relocated the question. A physicist, on the other hand, 'finds "causes" in what he has learned to recognize as fundamental properties... or unchanging laws, of matter and of energy.'

Today, Thompson would surely have to take up arms against the modern manifestation of the same Darwinian idea: genetics. It is not hard to become persuaded that in modern biology, all questions end with the gene. The pages of *Nature* and *Science* are filled with papers reporting the identification of a gene (or the protein derived from a gene) that is responsible for this or that biological phenomenon—for the development of a forearm, the predisposition to breast cancer, even for intelligence. The climate of the culture in molecular biology (although not, I think, the expressed belief of its individuals) is that, by understanding the roles of genes and the mutual interactions of the proteins derived from them, we will understand life.

This attitude finds expression, for instance, in the Human Genome Project, the international effort to map out every one of the 30 000 or so genes in the 23 chromosome pairs of the human cell. The first draft of this map was completed in 2000, and to judge from



some of the hyperbole it elicited, you would think that it has provided us with a complete instruction manual for the human body. But biologists know in their hearts that it does not provide this at all. We can certainly expect the genome map to reveal an awful lot about the way our cells work; and perhaps more importantly it will supply a tool that will greatly aid researchers studying genetically related diseases. That kind of information will be tremendously valuable for biomedical science.

Yet biological questions do not really end in the gene at all: they *start* there. It is easy to get the impression that once a gene for a particular congenital disease has been located, the problem is solved. But most genes are just blueprints for proteins, and the physiological pathology associated with the gene often results from some biochemical transformation that the protein does or does not facilitate. It might even result from some malfunction that shows up only several steps down the line from the behaviour of the gene product itself. Very often, if we are to make effective use of the information that genetics provides, we must figure out how the gene's protein product works, not just where the gene is. Biologists know this, of course, but I am constantly struck at how much of molecular biology advances at a 'black box' level, with little concern for the physical or chemical details of a biochemical process and an interest only in the *identity* of the genes and protein gene products that control it. The rest is, of course, truly the 'hard part' of biology (cynics might suggest that, now that chunks of human chromosomes can be patented and sold off, it is also the less profitable part). The crucial point, though, is that a gene itself might provide precious few clues about what this hard part entails.

Furthermore, organisms are *not* just genes and proteins made from them. There is goodness knows what else in the cell: sugars, soap-like molecules called lipids, non-protein hormones, oxygen, small inorganic molecules like nitric oxide used for cell communication, and minerals like the calcium hydroxyapatite of bone and tooth. None of these substances are encoded in DNA, and you would never guess, by looking at DNA alone, what role they play in the body. There are, furthermore, physical properties that biological structures possess, such as surface tension, electrical charge and viscosity. These are all relevant to the way that cells work, but gene-hunting cannot tell us much at all about what their role is.

In short, questions in biology of a 'How?' nature need more than genetics—and frequently more than a reductionist approach. If nature is at all economical (and we

have good reason to believe that this is usually so), we can expect that she will choose to create at least some complex forms not by laborious piece-by-piece construction but by utilizing some of the organizational and pattern-forming phenomena we see in the non-living world. If that is so, we can expect to see similarities in the forms and patterns of living and purely inorganic or physical systems, and we can expect too that the same ideas can be used to account for them both. It is in the undoubtedly truth of this idea that the spirit of *On Growth and Form* lies, and this is where the true pre-science of D'Arcy Thompson's achievement resides. Although I shall focus only occasionally on pattern and form in biology, I feel that this spirit pervades all of what I shall say in this book.

Is biology just physics?

It is not often that biologists develop simple models based on physical laws in attempting to explain what they see. And with good reason: it is very hard to take account of all of the multifarious factors that are important in living organisms. Biological systems are usually too delicate to rely on crude, general physical principles, and so biologists are wary of trusting to broad physical phenomena for explanatory purposes. To them, it feels uncomfortably like driving a car with no hands on the wheel, hoping that friction and air resistance will somehow conspire to guide the vehicle down a tortuous road.

It can be tempting, once one starts to appreciate the stunning variety of complex pattern and form in the natural sciences, to let the pendulum swing too far to the other extreme. A popular accusation against modern genetics is that it is too reductionistic, that one cannot understand all of the rich complexity of biology by breaking it down to genetic influences. One hears this again and again from proponents of 'holistic' science, who have no shortage of arguments to support their point of view—for certainly, one can find emerging from large populations of interacting 'units' (be they living organisms or non-living entities) a kind of large-scale organization and structure that one would never be able to deduce from a close inspection of the individual units or their mode of interaction. Such ideas, which have now become fashionable under the banner of 'complexity,' are often lauded as an injection of richness and mystery into the sterility of a reductionist world view.

I applaud a perspective that broadens the horizons of 'black-box' biology, but there is no getting away from the fact that most of biology, particularly as a molecular



science, is hideously *complicated*, which, in distinction to *complex*, means that the particulars matter: leave out one part of the chain, and the whole thing falls apart. In such a case, one gains rather than loses understanding as the magnification is increased. Until we get reductionistic about the immune response, let's say, we won't know much about it, and neither will we have much idea how to tackle pathological conditions such as AIDS. Reductionism can certainly be aesthetically unappealing, but it can also be fantastically useful. In addition, reductionism is not always the dogma it is cracked up to be. Richard Dawkins, whose books *The Selfish Gene* and *The Blind Watchmaker* are often invoked as the epitome of genetic reductionism, has stressed that his ideas by no means imply a kind of genetic determinism of biological form, characteristics and behaviour. Dawkins says only that it is the gene on which evolutionary forces ultimately act: that is, selection acts on the genotype (the organism's genetic composition), not the phenotype (the physical expression of that composition). There is nothing in what I shall say about biological form that is inconsistent with these notions.

But a few biologists, riding against the mainstream of current thought, hold a more extreme opposition to the genetic orthodoxy. Brian Goodwin from Britain's Open University has argued that a gene's eye view of modern biology cannot be complete, and that there are some fundamental aspects of an organism's form that persist *in spite of* natural selection, not because of it. Goodwin suggests that the pattern-forming principles seen in some non-living systems operate as strongly in living organisms, giving them features that evolution is powerless to erode away. I have to say that not many people believe Goodwin, although it seems to me that his arguments become weakened only when extended from specific instances to the status of a new developmental principle in biological growth. Insofar as I shall talk about biological form at all, the position I take is rather different. I don't think we know very much yet about whether natural selection has the power to modify or suppress certain pattern-forming principles that occur in nature. But I would suggest that, in the here and now, such principles undoubtedly exist—and do so in sharp distinction from the idea that genes are like a *deus ex machina* that holds all biological processes in thrall, building organisms in a laborious, brick-by-brick manner. To that extent, I don't believe I am saying anything that will disturb molecular biologists (although I think it a pity that they do not always regard these pattern-forming processes with a greater sense of wonder).

What is form?

This book is about the development of pattern and form, and so it is as well to have an indication of what I mean when I use these words. I cannot give either term a definition of mathematical rigour, however, nor can I always maintain a clear distinction between the two. There is always an element of subjectivity in perceiving patterns. On the whole I shall be concerned with patterns and forms in space, ones that we can see and perhaps touch. But of course there are all sorts of patterns—in a time sequence of events, in human behaviour and interactions, in stories and myths. The word is a very plastic one.

There are surely certain spatial images that most people would categorize as patterns—the repeating designs of wallpaper or carpets, for example. This prompts the idea that a pattern might be regarded as a regularly repeating array of identical units. I want to broaden that concept slightly, and include in my definition arrays of units that are similar but not necessarily identical, and which repeat but not necessarily regularly or with a well-defined symmetry. An example is the ripples of sand at the seaward edge of a beach or in a desert (Fig. 1.8). No two ripples are identical, and they are not positioned at exactly repeating intervals (which is to say, *periodically* in space)—but nonetheless, I don't think it is too hard to persuade ourselves that this might be reasonably called a pattern, as we can recognize within it elementary units (the ripples) that recur again throughout space. The ripples are usually all of more or less the same width; but I don't feel that even this need be essential to qualify as a pattern. A mountain range has features of all sizes, from little crevasses to huge sweeping valleys, but there is still something about the way it looks to us, from out of an aeroplane window, that allows us to see a pattern there.

Form is a more individual affair. I would define it loosely as the characteristic shape of a class of objects. Like the elements of a pattern as described above, objects with the same form do not have to be identical, or even similar in size; they simply have to share certain features that we can recognize as typical. Shells of sea creatures are like this. The shells of organisms of the same species all tend to have a certain form that can be recognized and identified even by a relatively untrained eye, despite the fact that no two shells are identical. The same is true of flowers, and of the shapes of mineral crystals. The true form of these objects is that which remains after we have averaged away all the slight and inevitable variations between individuals.

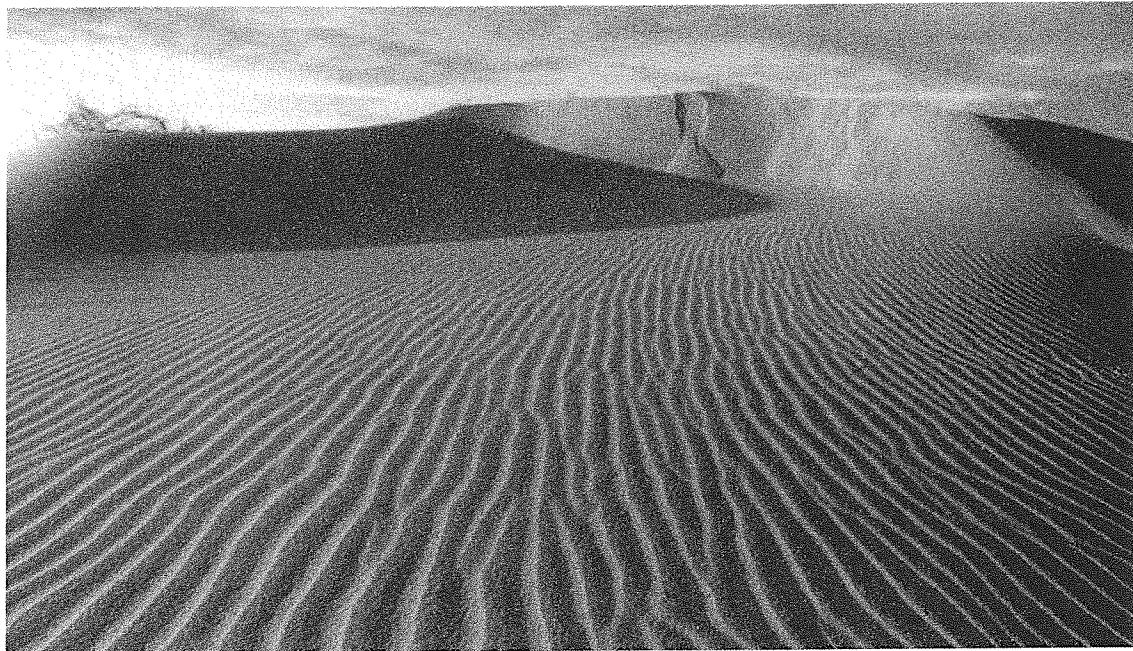


Fig. 1.8 Ripples in sand are self-organized patterns formed by wind-blown sand transport. (Photo: Nick Lancaster, Desert Research Institute, Nevada.)

Patterns, then are typically extended in space, while forms are bounded and finite. (But take this as a guideline, not a rule.)

Symmetry and order are related but not synonymous. Complex natural forms commonly have the appearance of a kind of order even when, mathematically speaking, they have very little symmetry. An oak tree, for instance, has as little symmetry as it is possible for an object to possess, but is it disorganized? It is often said of symmetry that our intuition is at odds with a mathematical description. Which is more symmetrical—a kaleidoscopic image like that in Fig. 1.9a or a six-pointed Star of David (Fig. 1.9b)? We might say that the kaleidoscope pattern has more organization, more repeating features; but mathematically the symmetries of both images are the same. And are either of these more symmetrical than a circle? No, they're not—the circle has the highest possible degree of symmetry for a two-dimensional (flat) object. It's just that we don't perceive the symmetry so readily when it becomes as great as it is in a circle—to us that just looks bland and featureless. I don't propose to say much more about symmetry *per se*, because there are many splendid books that deal with this endlessly fascinating topic, of which Hermann Weyl's *Symmetry* is a classic and *Fearful Symmetry* by

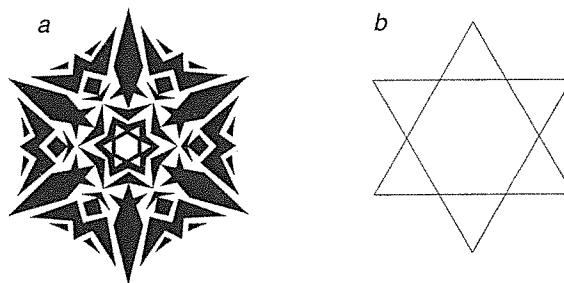


Fig. 1.9 The formal symmetry of these two patterns is the same, even though (a) looks much more complex than (b).

Ian Stewart and Martin Golubitsky is one of the most up-to-date and lucid.

The natural language of pattern and form is mathematics. This may dismay those of you who never quite made friends with this universal tool of science, and it may seem a little disappointing too—for patterns and forms can be things of tremendous beauty, whereas mathematics can often appear to be a cold, unromantic and, well, calculated practice. But mathematics has its own very profound beauty too, and this is something that you do not any longer have to take on trust. The now familiar images of fractal forms and patterns



demonstrate that mathematics is perfectly able to produce and describe structures of immense complexity and subtlety.

The main point is that mathematics enables us to get to grips with the *essence* of pattern and form—to describe it at its most fundamental level, and thereby to see most clearly what features need to be reproduced by an explanation or a model. In short, the mathematical description of a form can be considered to pertain to that which is left after the particular irregularities or anomalies of any individual example of that form (for example, the small imperfections or bumps on a shell) are averaged out. To explain how the form of the shell arises, there is no point in trying to explain all the little bumps, since these will be different for each shell; we need instead to focus on the ‘ideal’ mathematical form. This concept of an ideal, perfect form behind the messy particulars of reality is one that is generally attributed to Plato.

Why does maths help us in this endeavour? For a start, it provides a very concise and precise description of a form. Try to describe a circle in words, without using any of the pre-existing associations of circular objects (such as ‘the shape of a full moon’). It is ‘round all over’, but isn’t that also true of an egg or a sea-smoothed pebble? And if you had to *construct* a circle without exploiting its mathematical features (which I am just coming too), you’d have an even harder time. The French mathematician Pierre Laplace was famously able to draw a perfect circle freehand, but this ability is not granted to most of us.

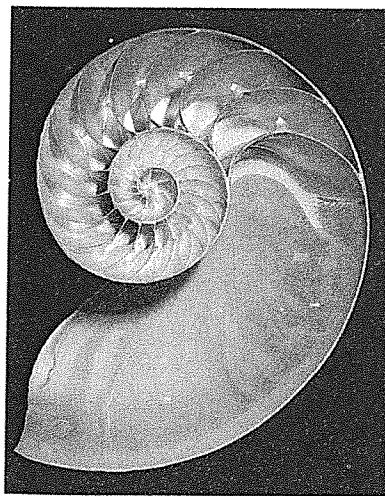
The mathematical description of a circle, meanwhile, can be expressed in words as ‘a line in a flat plane that is everywhere an equal distance from a single point’. If that doesn’t strike you as particularly concise, let me quickly indicate the symbolic depiction of this definition in mathematics:

$$x^2 + y^2 = R^2 \quad (1.1)$$

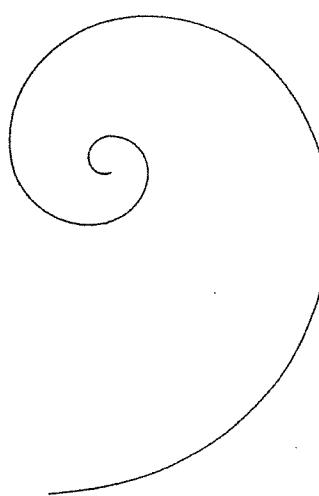
Not only does this help us to express exactly what a circle is; it also suggests immediately how we might construct one. You need only to keep your pen a constant distance from a point on the paper, for example by attaching its end to a piece of string anchored at the other end by a pin. The way to ‘grow’ a form often becomes obvious once the form is described mathematically.

This is a point that comes out with great force and clarity from D’Arcy Thompson’s work. If you look at a mollusc shell (Fig. 1.10a) and try to imagine how the cluttered frenzy of the cell could put together such a gracefully spiralling object, or conversely how it might have arisen by chance through evolution and natural selection, you may be forced to conclude that the problem is profound. But once you recognize that the shell has a precise mathematical form—that of a so-called logarithmic spiral—then you begin to see that nothing more than a simple and plausible growth law is required.

The logarithmic spiral (Fig. 1.10b) was first characterized mathematically by René Descartes in 1638. It is



a



b

Fig. 1.10 The shells of snails and other molluscs (a) trace out logarithmic spirals (b). (Photo: Scott Camazine, Pennsylvania State University.)



defined as the curve traced out by a point rotating around a point of origin with constant angular velocity (that is, it always takes the same time to rotate through the same angle), while its linear speed at any instant increases in direct proportion to its distance from the point of origin. That probably does not sound particularly elegant or concise, but the symbolic expression can be made extremely neat:

$$r = a^\theta \quad (1.2)$$

This three-symbol formula might leave you none the wiser, but you can't deny its concision. And to a mathematician, it conveys precisely the same information as the curve in Fig. 1.10b.

The logarithmic spiral has the unique property that the curve is everywhere 'similar', differing in size but not in shape. In other words, as the curve rotates through a fixed angle, it grows uniformly in scale. This, and the description above, help us to see what are the fundamental generating mechanisms of such a form. Some things remain constant, for example the angular speed of the curve's tip, and the shape of the curve, while other things, for example the linear (tangential) speed of the tip, change in a well-defined way. We can then generate a form like this by proposing that the deposition of new fabric at the shell's rim follows a growth mechanism that produces these characteristics. A mechanism of this sort that generates a three-dimensional mollusc shell with the cross-section of a logarithmic spiral is as follows: the existing shell rim provides a template on which new shell material is laid down, so it stays the same shape, but the rim is expanded in *scale* at a constant rate. If, in addition, the growth happens initially to be slightly faster on one side of the embryonic rim than the other, this imbalance is maintained proportionately as the shell gets bigger, and it curves into a spiral. It does not take too much imagination to see that a mechanism like this is a rather 'natural' one to be expected from a creature making a shell that needs to keep pace with its own growth, and doesn't require any mysterious geometrical knowledge or an ability to figure out what on earth equation 1.2 means. The imbalance that leads to spiral growth could come from any source—any imbalance will produce a logarithmic spiral. If there is no imbalance, the shell instead has a cone shape, just as one can find in some species of mollusc.

You might be able to appreciate too that a growth mechanism this simple need not be restricted to shells, but could apply to any hard tissue whose shape is determined purely by the deposition rate at the growing edge.



Fig. 1.11 Many animal horns, like those of this male Dall's sheep, are logarithmic spirals.

Horns too are commonly logarithmic spirals, albeit often more gently curving (Fig. 1.11). So we can anticipate these forms too as the expected result of an obvious growth mechanism, rather than as a form selected at random from a huge range of others by natural selection.

Let's look at another way that the logarithmic spiral, the ideal form of sea shells, illustrates how mathematics helps us to get to the essence of form and to make its explanation a much simpler process. D'Arcy Thompson realized that even very complex shells have a form that can be generated by the logarithmic spiralling of a certain fixed two-dimensional shape (later called the generating curve). He said,

The surface of any shell may be generated by the revolution about a fixed axis of a closed curve, which, remaining always geometrically similar to itself, increases its dimensions continually The scale of the figure increases in geometric progression [exponentially in time] while the angle of rotation increases in arithmetical [at a constant rate].

This is illustrated in Fig. 1.12. Thompson noted that the form of the generating curve 'is seldom open to easy mathematical expressions—but the way in which the shell shape is created by sweeping this curve in a spiral through space is mathematically well-defined, and can be imagined to be a consequence of a simple growth law. With this concept in mind, an explanation for the form of any particular kind of shell reduces to an explanation of the shape of the generating curve—the whole myriad of shell forms can be produced by the same kind of spiral evolution of these two-dimensional boundaries. Deborah Fowler and Przemyslaw Prusinkiewicz at the University of Regina in Canada have used computer-modelling to depict some of the shapes that result by taking a given

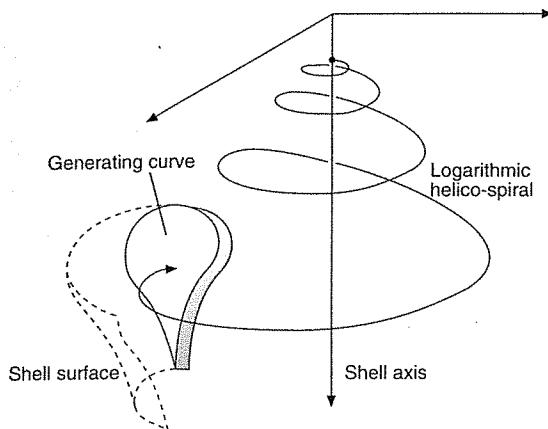


Fig. 1.12 A shell surface can be constructed by sweeping a two-dimensional 'generating curve' through a logarithmic spiral pulled out into a helix.

generating curve through the mathematical paces outlined by Thompson (Fig. 1.13).

The real advantage of using mathematics to describe form is that it makes the problem *algorithmic*. An algorithm is a sequence of logical steps that a computer program, say, must execute to carry out a certain task. Complex shapes like those seen here are often most easily described not in terms of 'what goes where' but by an algorithm that generates them. Once we know the mathematical algorithm, we can start to ask what kind of physical processes might provide a form-generating

rule to which the algorithm is a good approximation. In this way, the mystery of complex form and pattern becomes much more clearly defined.

Model making

I'll say much in this book about models. In everyday terms the word commonly implies 'a small-scale replica of the real thing' (although fashion models might take exception to this). To scientists, a model is something rather different. When science seeks explanations, it doesn't usually expect them to be exhaustive. On occasion that's simply because we don't know everything that is going on in the system we're looking at. In other cases it may be because we know that some influences are of little significance, so that their inclusion would just make the equations harder to solve without altering the solutions very much. Or again, it may be that certain influences are known to be important but we don't know *how* to include them, or how to solve the equations if we do. So then we look for good approximations that we *can* solve, knowing that the answers might not correspond quite so well with observations. Biology operates quite a lot of the time within the first of these scenarios—we don't know enough about the details. A lot of engineering is conducted in the spirit of the second situation—one might ignore the effect of air resistance or of friction in figuring out the way an object moves. (Galileo did the same in his famous—and apocryphal—experiment from the Tower of Pisa.) But engineers who worry about problems of

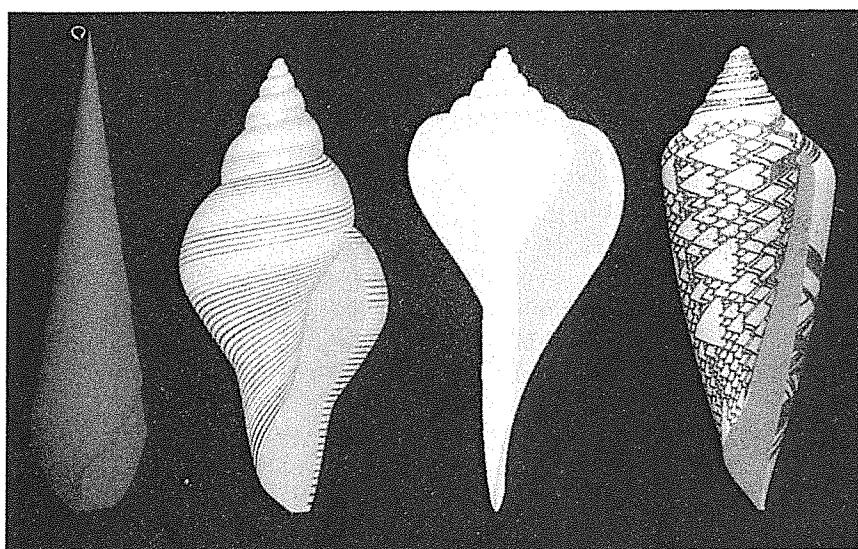


Fig. 1.13 Shells created on a computer by applying the 'algorithm' depicted in Fig. 1.12 to a variety of generating curves. (Images: Deborah Fowler and Przemyslaw Prusinkiewicz, University of Calgary, Canada; from Meinhardt (1995).)



Box 1.1: Exponents

Although mathematics provides the natural language for talking about patterns, I will not need to use in this book any more mathematics than can be expressed in words rather than in abstruse equations. You will need to know little more than the definition of squares and cubes of numbers. The square of 2, written 2^2 , is 2×2 , and the cube (2^3) is $2 \times 2 \times 2$. The superscripted number is often called the *power* or *exponent*: 2^3 , for

instance, might be called ‘two to the power three’. We will at a later stage be confronted with rather more curious mathematical entities in which the powers are not whole numbers, such as $2^{2.26}$. It is not clear how to write that in multiplicative longhand, but you need know only that this quantity has a well-defined numerical value, that there are rather simple mathematical ways (involving logarithms) to calculate it, and that its value is greater than 2^2 (= 4) and less than 2^3 (= 8).

fluid flow (a topic discussed in Chapter 7) commonly find themselves in the third situation—making big approximations and accepting the consequences.

The point is that scientific descriptions of phenomena in all of these cases do not fully capture reality—they are models. This is not a shortcoming but a strength of science—much of the scientist’s art lies in figuring out what to include and what to exclude in a model, and this ability allows science to make useful predictions without getting bogged down by intractable details.

Now, the thing that is not often stressed or appreciated about scientific model-building is that there are very many natural phenomena (one could make a strong case for this being true of them all, in fact) for which there is not a single, unique model that is ‘right’. This is more than a matter of models differing by the choice of what to put in and leave out, as though all are assembled in a modular fashion. Rather, some phenomena can be tackled successfully from more than one entirely different perspective. This is true of several of the phenomena that I shall discuss in this book.

A particularly common distinction is that between *numerical* and *analytical* models. Computers are so sophisticated nowadays that complex physical processes, such as the freezing of a liquid, can be simulated computationally by simultaneously solving the equations of motion for thousands or even millions of simulated molecules. This is a numerical model, in which the behaviour of the entire system emerges from the piece-meal enumeration of the behaviour of each of its component parts. An analytical model of the same process, in contrast, might make no attempt to describe the motion of individual particles, but will involve mathematical expressions for the relationships between different bulk properties of the medium, such as temperature, density and energy. It may even be possible to solve such a model with pen and paper (which was all theorists had at their disposal up to half-a-century ago).

Although these two approaches are very different,

they might both include (and exclude) in their recipes exactly the same physical forces and parameters. But other models might differ in their essential ingredients—we’ll encounter later, for instance, two models for the growth of bacterial colonies, one that assumes that the bacteria repel each other and another that assumes only attractive interactions between cells. The problem is that is it not uncommon to find that two models differing like this will generate more or less the same apparent behaviour! The trick is then to find under what conditions the models *do* generate different results, and to try to conduct experiments under those conditions in order to decide which model to favour. This is a familiar challenge in the sciences of pattern formation.

Perhaps the strongest point that I want to make about models in the present context is that they can often generate the complex patterns seen in nature from remarkably few ingredients, which are themselves of striking simplicity. OK, you might say, it’s not obvious that this should be so—but what does it mean? Well, on one level it means that growth and form need not be mysterious—we do not have to resign ourselves to thinking that the shape of a flower will be forever beyond our abilities to explain, or even that an explanation (at some level) will require years of dedicated research on plant genetics. On the other hand, it carries at least an implication that there exist universal patterns and forms which remain robust to the fine details of a particular system. For the simple rules of these models are typically of a general nature: ‘Assume that the particles move about at random’, for instance, not ‘Assume that the ETS domain protein encoded by the P2 transcript of the *pointed* gene is a nuclear target of a signalling cascade involving Ras1 and Raf which acts downstream of R1/MAP kinase’.*

* That’s a direct quote, by the way, more or less. I don’t mean to imply that this kind of research is absurd, but just that nature can be, as far as we are concerned, absurdly complicated.



Thus a single model, and its adherent patterns and forms, may turn out to be applicable to a number of different real phenomena.

Breaking the monotony

It's not unusual to associate pattern with order: creating a recognizable pattern rather than a mess requires an orderly process of putting the pieces in place. It is, then, possibly a little alarming to discover that in nature the most highly symmetrical systems are also the most random.

As I mentioned earlier, we often don't perceive any pattern in the most symmetrical systems: they are uniform and, to our minds, featureless. In nature, however, nothing is truly featureless if you look close enough. All matter is made up of atoms, and at the scale of less than a millionth of a millimetre this graininess becomes apparent and the illusion of a uniform medium is lost. Physicists generally regard gases and (to a lesser degree) liquids as uniform, fully symmetrical systems. Yet on the atomic scale all one sees is random disorder, atoms and molecules whizzing about with no apparent symmetry at all. The uniformity and high symmetry become apparent only by considering the *average* features of these systems, which we can do either by focusing our attention on one region and averaging the molecular motions over time or by comparing a large number of different regions at any instant. In both cases, a gas then appears to have a completely uniform density of molecules, on average, at all points in space (it is *homogeneous*); and they travel in all directions with equal probability (the gas is *isotropic*).

When this randomness is absolute, the highest symmetries are observed. (By 'higher symmetry' I mean that the system has a greater number of transformations, such as rotations around an axis or reflections in a mirror plane, that leave it looking the same.) That is why a soap bubble is spherical: its perfect symmetry is a consequence of the fact that the pressure of gas inside the bubble is equal in all directions, because on average an identical number of gas molecules collide with the bubble walls at all points.

The problem of creating patterns and forms that we tend to recognize as such is therefore not one of how to generate the symmetry that they often possess, but of how to *reduce* the perfect symmetry that total randomness engenders, to give rise to the lower symmetry of the pattern. How do the water molecules moving at random in the atmosphere coalesce into a six-petalled snowflake? Patterns like this are the result of *symmetry-breaking*.

The symmetry of a uniform gas can be broken by applying a force. Gravity will suffice: in a gravitational

field the gas is denser where the field is stronger (closer to the ground). Thus the atmosphere has a density that increases steadily towards ground level. The gas is then no longer homogeneous or isotropic. In this example, the symmetry of the force dictates the symmetry of the distribution of matter that it produces: gravity acts downwards, and it is only in the downwards direction that symmetry is broken. Within horizontal planes (more properly, concentric spherical shells around the Earth) a constant distance from the ground, the atmosphere has a constant density (well, it *would* have if the Earth were a perfect sphere and there were no winds). We might intuitively expect that this will always be so: that the final symmetry of a system will be dictated by that of the symmetry-breaking force that destroys an initially uniform state. In other words, we might expect that matter will rearrange itself only in the direction in which it is pushed or pulled. Within this picture, if you want to pile up sand into mounds arranged in a square, checkerboard array, you will have to apply a force with this 'square' symmetry.

But it is the central surprise of the science of pattern formation that this is not necessarily so. The symmetry of a pattern formed by a symmetry-breaking force does *not* always reflect the symmetry of that force. Of the many examples that I shall describe throughout this book, one will serve here to illustrate what I mean, and why this seems at first sight to be astonishing. If you heat (very carefully—it is not an easy experiment in practice) a shallow pan of oil, it will develop roughly hexagonal circulation cells once the rate of heating exceeds a certain threshold (Plate 1; see also Appendix 1). The system (the fluid) was initially uniform in the plane of the pan, and the symmetry-breaking force (the temperature difference between the top and bottom of the fluid layer) was also applied uniformly in this plane—yet suddenly this uniformity is lost, being replaced by a pattern with hexagonal symmetry. Where has this sixfold pattern come from?

In such cases, one is apparently getting 'order for free'—getting order out without putting order in—although as I say, it is more correct to say that symmetry is being lost rather than gained. The central questions behind many pattern-forming phenomena are: how is it that symmetry can be spontaneously broken? How can the symmetry of the effect differ from that of the cause? And why is symmetry so often broken in similar ways in apparently very different systems? That is to say, why are some patterns universal? These are questions profound enough to last us throughout the rest of the book.