Hits, Misses and Close Calls:
An Image Essay on Pattern Formation in *On Growth and Form*

Philip Ball

[A version of this article is published in *Interdisciplinary Science Reviews* **38.1**, 74-88 (2013)]

The second edition of D'Arcy Thompson's *On Growth and Form* was written only shortly before the advent of computers made it possible to develop more sophisticated mathematical models of processes of growth, morphogenesis and pattern formation in nature. It also predates the blossoming of several branches of science with the conceptual tools to investigate complex phenomena such as self-organization, nonlinear dynamics and chaos, fractal geometry and self-organization. As a result, Thompson's aspirations sometimes fall short of his means – and occasionally he sets out on the wrong path. This image essay explores some of the instances in which Thompson surpassed his limitations, or alternatively was constrained by them. In either circumstance, it illustrates how his themes remain areas of significant scientific activity today.

Animal markings: spots and stripes

While it is often rightly said that D'Arcy Thompson would have benefitted from a computer, many of the lacunae, abandoned and half-hearted explanations in *On Growth and Form* (*OGF*) stem from a lack of conceptual rather than computational tools. That is true in the case of one the most fertile theories of pattern formation, formulated ten years after the revised edition of the book was published in 1942. The markings on the skins of animals – the spots of the leopard and stripes of the zebra – were almost literally an afterthought for Thompson, who admitted after a thousand pages that "*pattern* has been wellnigh left out of the account, although it is part of the same story" [*1090*; hereafter, italicized page numbers refer to *OGF* 2nd edition [1]]. Thompson goes on simply to enumerate the various characteristic ways in which a zebra's stripes adapt to the body shape – the chevrons at the juncture of foreleg and torso, the 'gridiron' of the rump (Figure 1). No real explanation for these markings is even attempted.

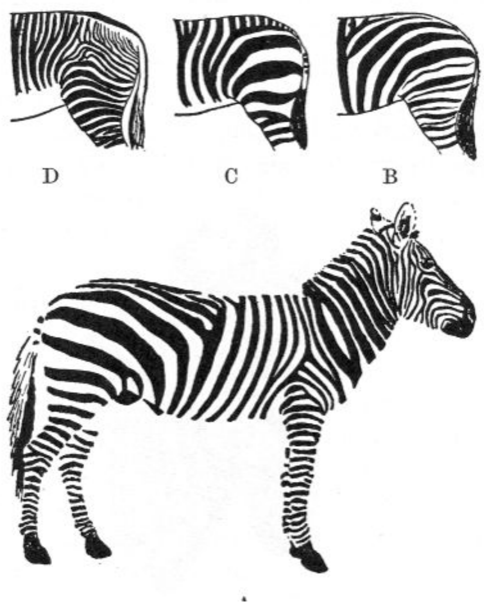


Figure 1 Zebra patterns from *OGF* [*1092*].

In essence they were accounted for, however, in 1952 in a paper by Alan Turing titled "The chemical basis of morphogenesis" [2]. Turing devised his theory primarily to account for the asymmetric division of a spherically symmetric embryo into regions with different developmental trajectories as the body plan emerges. This is an example of the phenomenon that physicists recognize as spontaneous symmetry-breaking: the reduction in symmetry that commonly accompanies the appearance of complex form. Turing postulated (bio)chemical agents called morphogens that diffuse through the embryo and condition cells to form different tissues. It later became clear that diffusing morphogens with particular chemical characteristics – specifically, ones that are autocatalytic, speeding up their own rate of formation in a feedback process – can in some circumstances create regions of distinct chemical composition in an abiotic chemical system. This combination of diffusion, which tends to equalize differences of composition, and autocatalytic reaction, which tends to exacerbate them, is the distinguishing feature of what is now known as a reaction-diffusion system.

Turing showed, in effect, that a particular subset of reaction-diffusion equations can generate a fixed, non-uniform spatial pattern from an initially uniform mixture of morphogens. He realised the possible relevance for animal markings but, lacking a computer (his ideas were of course central to the development of these machines in the 1950s), he could only sketch out a rough indication of the patchiness of his system from calculations performed by hand. Later computational studies showed that these so-called Turing patterns have the characteristic forms of spots and stripes (Figure 2), being quasi-ordered in the sense of having a more or less uniform size and spacing but lacking perfect periodicity. The application of these ideas to animal markings was pioneered in the 1970s and 1980s by mathematical biologists James Murray [3] and Hans Meinhardt [4], who showed that Turing's mechanism, enacted with morphogens that control pigmentation, can produce patterns ranging from zebra stripes and leopard spots to markings on mollusc shells [5] (Figure 3).

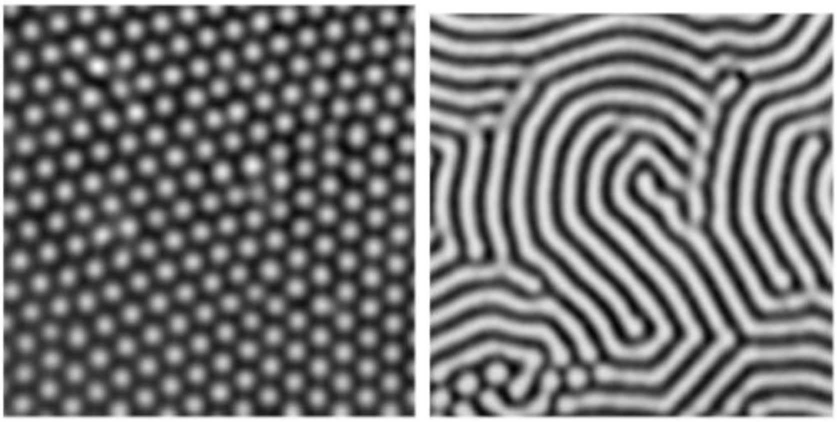


Figure 2 The generic patterns of Alan Turing's activator-inhibitor scheme: spots and stripes. Images: Jacques Boissonade and Patrick De Kepper, University of Bordeaux.

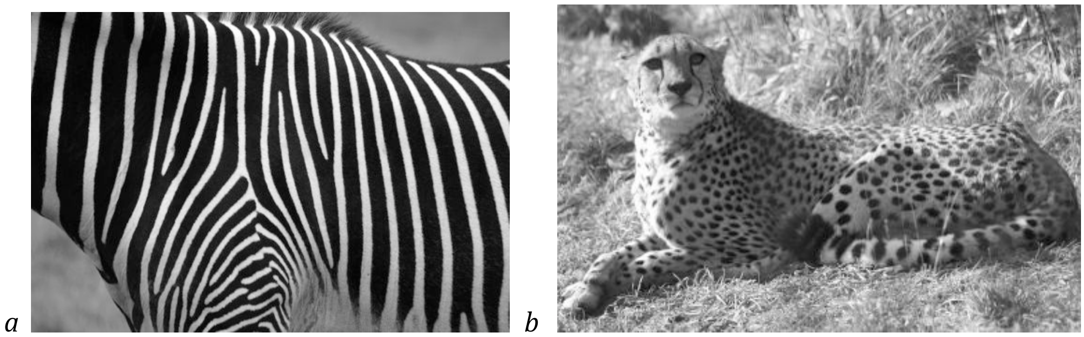


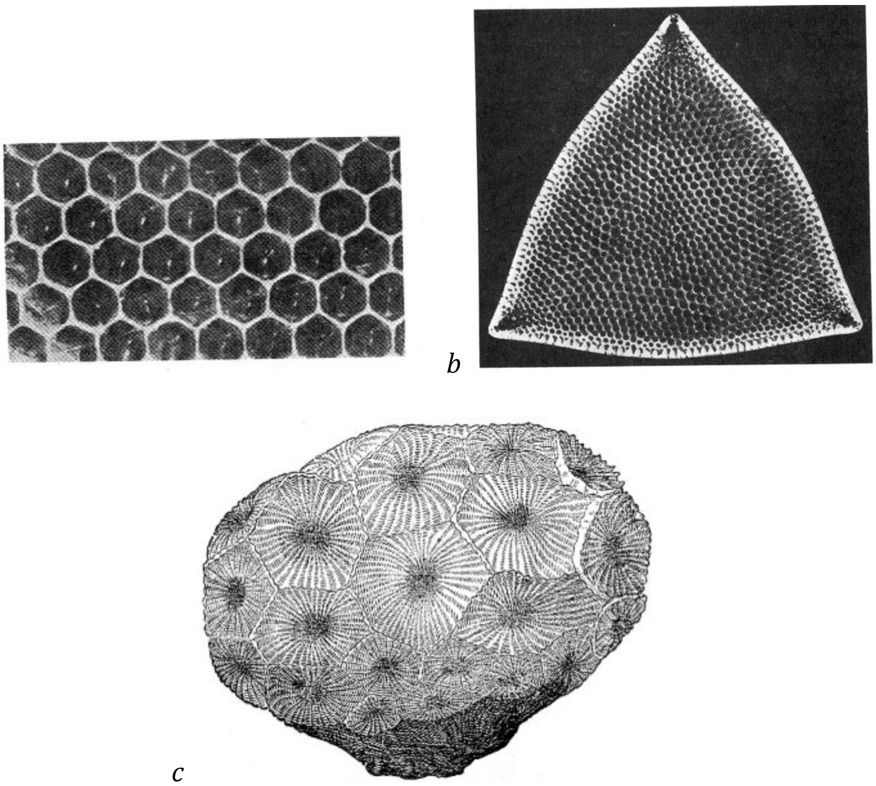
Figure 3 Markings on zebras (*a*) and leopards (*b*) seem likely to be variants of Alan Turing's chemical patterning mechanism. Images: *a*, Martin Pettitt; *b*, Andy Rogers.

Turing's mechanism is a very general one, requiring only dispersal and feedback (positive and negative, or 'activating' and 'inhibitory') of the interacting constituents within a particular range of parameters. It has been proposed as an explanation for the patchiness of some ecosystems, the spatial regularities of animal habitats, and even the formation of ripples in windblown sand (Figure 4) [5].

Figure 4 Ripples in windblown sand can be considered the product of an activator-inhibitor process like that postulated by Turing. Image: .EVO.

Convecting fluids

The spontaneous creation of two-dimensional hexagonal patterns is so common in nature that it seemed natural to Thompson to consider such structures in a unified way – from bubbles and honeycombs to the biomineral mesh of diatom exoskeletons (Figure 5) and the Giant's Causeway (see below). Mechanics and simple geometry will suffice, he suggested, to produce such an arrangement in most if not all cases. Consider, for example, a layer of growing spherical or circular cells of uniform size. The most efficient packing is hexagonal, and the internal pressure will push the boundaries into hexagons as they come into contact. Surface tension will perform that task for soap bubbles; and as for the honeycomb, Thompson points out how Erasmus Bartholin in the seventeenth century proposed that "the hexagonal cell was no more than the necessary result of equal pressures, each bee striving to make its own little circle as large as possible." [*527*] The fact that the hexagonal array minimizes surface area, and thus economizes on wax, then becomes incidental.



a *b* *c*

Figure 5 Some of the hexagonal and polygonal patterns considered by D'Arcy Thompson: honeycombs (*a*) [*527*], diatom exoskeletons (*b*) [*511*], and coral (*c*) [*513*].

But Thompson was wrong about bees, which cannot rely on self-organizing physics but must build their hexagonal cells by exquisite measurement of angles and wall thickness – and after all seemingly mindful of the economics. Some of Thompson's other examples turn out to be a little more subtle too. He was struck by the polygonal, pseudo-hexagonal arrays formed by processes of diffusion, as investigated by the French biologist Stéphane Leduc – the "artificial cellular tissues" made by coloured drops of sodium chloride in salt solution or by potassium ferrocyanide in gelatine (Figure 6). He paid particular attention, however, to the "*tourbillons cellulaires*" studied in 1900 by the French physician Henri Bénard (Figure 7), which appear in a thin liquid layer heated from below so that it undergoes convective flow [6]. Thompson points out that the German Heinrich Quincke had reported the same patterns 30 years earlier. Convection currents are produced as the lower liquid becomes warmer and less dense, and begins to rise by buoyancy:

> The liquid is under peculiar conditions of instability, for the least fortuitous excess of heat here or there would suffice to start a current, and we should expect the system to be highly unstable and unsymmetrical… [but] whether we start with a liquid in motion or at rest, symmetry and uniformity are ultimately attained. The cells draw towards uniformity, but four, five or seven-sided cells are still to be found among the prevailing hexagons… In the final stage the cells are hexagonal prisms of definite dimensions, which depend on temperature and on the nature and thickness of the liquid layer; molecular forces have not only given us a definite cellular pattern, but also a "fixed cell-size"… When bright glittering particles are used for the suspension (such as graphite or butterfly scales) beautiful optical effects are obtained, deep shadows marking the outlines and the centres of the cells [*503*].

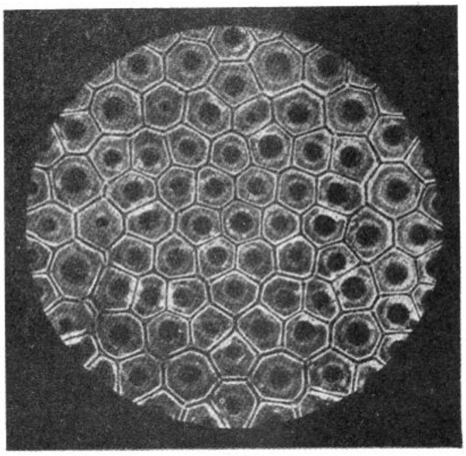


Figure 6 An 'artificial cellular tissue' formed from potassium ferrocyanide diffusing in gelatine [*501*].

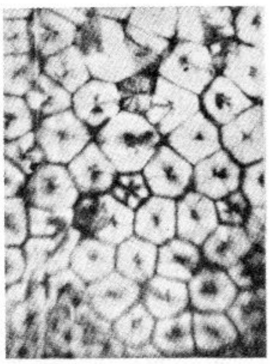


Figure 7 Bénard's convection patterns or *tourbillons cellulaires* in smoke [*504*].

This technique of using 'tracer' particles to map out fluid flow, first mentioned by Leonardo da Vinci, has produced some very beautiful images of hexagonal convection cells in modern experiments (Figure 8). Thompson perceptively points out that where we might expect turbulent chaos, we get geometric order, and moreover that there is a selection process that determines the size of the pattern features.

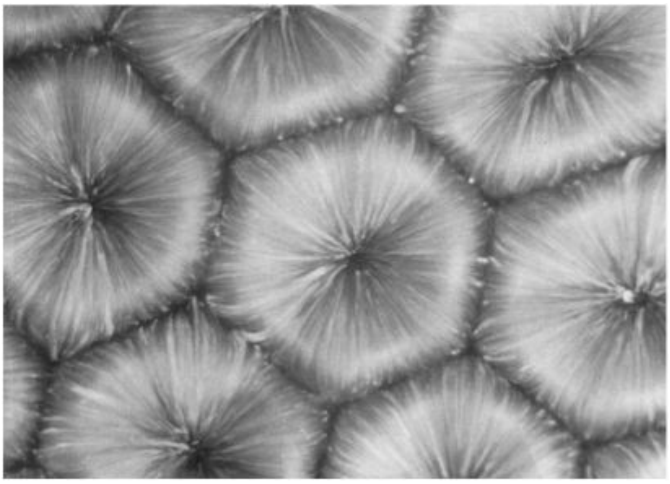


Figure 8 A hexagonal convection pattern rendered visible by suspended metal flakes. Image: Manuel Velarde, Universidad Complutense, Madrid.

He explains that this phenomenon was studied theoretically by Lord Rayleigh in 1916, who showed that patterned convection only appears above a particular threshold in temperature gradient [7]. They represent another case of symmetry-breaking: the fluid is initially uniform in the plane of the surface, but breaks up into regions of ascending or descending flow. Rayleigh found that initially convection creates not hexagons but parallel 'roll cells', looking from above like stripes. How this pattern evolves as the heating rate increases is a very subtle matter: the mathematical analysis of the stability of different cell shapes is complicated, and was performed only in the 1960s and 1970s by Friedrich Busse and his coworkers. Convection can produce patterns not only in liquids but in, for example, 'frost-heaving' of stones during freeze-thaw cycles of frozen ground (Figure 9*a*) and the regular patterning of clouds in the atmosphere (Figure 9*b*) – both also structures noted by Thompson.

a

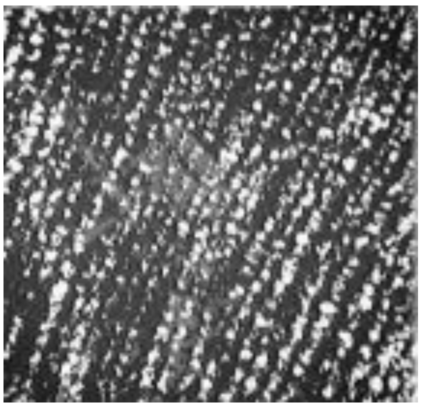

b


Figure 9 Convection is believed to create stone polygons in the soils of northern tundra (*a*) and the regular striations of cloud streets (*b*). Images: *a*, Agriculture and Agri-Food Canada; *b*, NOAA, Boulder, Colorado.

Phyllotaxis

The spiral ordering of some plant structures, such as the florets of a sunflower or cauliflower head (Figure 10), could hardly escape the attention of any natural philosopher, and has long been remarked on: as Thompson pointed out, the Royal Society's botanist and cataloguer Nehemiah Grew claimed in his seminal *Anatomy of Plants* (1683) that "from the contemplation of Plants, men might first be invited to Mathematical Enquirys" [*912*]. The history of this topic, called phyllotaxis, is long, and includes such figures as Leonardo da Vinci, the Swiss botanist Charles Bonnet, the French mathematicians Louis and Auguste Bravais, and Charles Darwin.

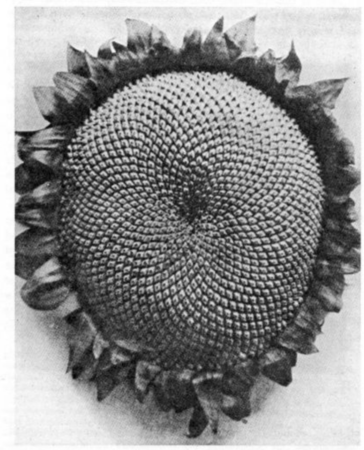
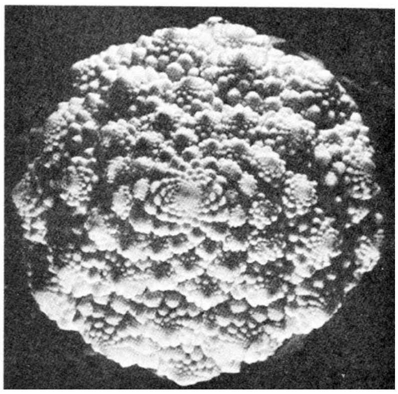



Figure 10 Phyllotaxis in the sunflower and cauliflower [*913, 914*].

The most celebrated property of phyllotactic patterns is the numerical relationships of the spirals. There is a set that rotates clockwise and another rotating counterclockwise, and invariably – on the pine cone, the sunflower, the monkey-puzzle tree and elsewhere – the numbers of spirals in the two sets are successive members of the Fibonacci series. Attributed to the thirteenth-century Italian mathematician Leonardo of Pisa ('Fibonacci'), this is a sequence in which each member is the sum of the previous two, beginning with 0 and 1: 0, 1, 1, 2, 3, 5, 8, 13, 21, 34... The ratio of successive terms approaches a constant the further one progresses along the series: an irrational number known as the Golden Section and equal to $2/(\sqrt{5}-1) = 1.618034$ to the first six decimal places.

Why should phyllotaxis show this apparent numerology? Thompson argued that the spirals *per se* are an entirely predictable consequence of orderly packing of elements accompanied by growth in one direction: "When the bricklayer builds a factory chimney, he lays his bricks in a certain steady, orderly way, with no thought of the spiral patterns to which this orderly sequence inevitably leads" [*921*]. He argues on geometric grounds that, given this spiral form, the Fibonacci relationships are simply those that ensure "no leaf should be superimposed above another" [933]. He has no time for quasi-mystical suggestions that the plant is "aiming" to position its leaves or florets at some "ideal angle."

Maybe so; but there does seem to be a possible optimization process at play here. The German botanist Wilhelm Hofmeister proposed in 1868 that each new leaf bud (primordium) appears periodically on the boundary of a growing stem apex in a position corresponding to the largest gap left by the preceding primordia [8]. In other words, the primordia are simply trying to pack efficiently, just like atoms in a crystal. In 1904 Arthur Church, an English botanist, took this idea further in a book called *On the Relation of Phyllotaxis to Mechanical Laws*, drawing on rather vague comparisons with spiralling vortices in fluid flow and magnetism and proposing that the "energies of life" resemble electrical energy [9]. D'Arcy Thompson dismissed such ideas: "[Church's] physical analogies are remote, and the deductions I am not able to follow." [*920*]

Nonetheless, Hofmeister and Church did help to establish the idea that phyllotaxis is related to the question of how new leaves can be packed on the stem apex. This notion has defined most modern thinking on the matter. The thesis was supported by computer calculations showing that if successive spiralling primordia diverge at the "Golden Angle" of 137.5°, they are optimally packed [10].

But packing alone will not suffice, for even small errors (inevitable in a biological growth process) will disrupt it. There seems in fact to be a genuine repulsion between primordia. This was implied by experiments in which repelling droplets of a magnetic fluid added successively to a disk and travelling towards the outer edge adopt a phyllotactic arrangement [11]. Meanwhile, studies in the 1930s showed that a plant stem's apex actively *inhibits* primordium formation within a certain distance. This inhibition can be attributed to diffusion of the hormone auxin through the outer 'skin' of the stem, which may engage in the activation and inhibition of proteins involved in primordium development [12]. If this process of chemical inhibition recalls Turing's activator-inhibitor scheme, that is appropriate. It seems possible that the patterning process in plants is indeed formally akin to those in animal markings [13] – just, in fact, as Alan Turing suspected. [14]

The Giant's Causeway

The quasi-geometric columns that may be formed in volcanic basalt have long been regarded with wonder. When the botanist Joseph Banks visited Fingal's Cave on the island of Staffa, off Scotland's west coast, in 1772, he was amazed by the geometric facility of nature (Figure 11). "Compared to this", he said,

> what are the cathedrals or palaces built by men! Mere models or playthings, as diminutive as his works will always be when compared with those of nature. What now is the boast of the architect! *Regularity*, the only part in which he fancied himself to exceed his mistress, Nature, is here found in her possession, and here it has been for ages undescribed [15].

Figure 11 The entrance to Fingal's Cave, Staffa, Scotland. Image: Stephen Morris, University of Toronto.

Thompson shows the same geological pattern at the Giant's Causeway in County Antrim, on the coast of Northern Ireland (Figure 12). He explained that these rock formations appear in basaltic lava as it cools, contracts and cracks: "rupture… shatters the whole mass into prismatic fragments", he wrote. "However quickly and explosively the cracks succeed one another, each relieves an existing tension, and the next crack will give relief in a different direction to the first." [*521*] This is all very fine, but Thompson does not really account for why the cracks create such a remarkable pattern: a series of vertical columns, each with a polygonal cross-section that seems most often to be hexagonal.

Figure 12 The Giant's Causeway, Country Antrim [*520*].

The cracking of the Giant's Causeway began at the top – where the heat of the molten basaltic outflow escaped and the lava was therefore coolest – and advanced downwards into the solidifying rock bed. This occurred in a succession of layers, each freezing and cracking before the next, which has left horizontal striations in the surfaces of the basalt pillars.

In 1983 the Irish physicists Denis Weaire and Conor O'Carroll suggested that irregular cracking of the uppermost layers would become marshalled into a stable polygonal network as the cracks descend, because, for a fixed total length of cracks, a polygonal, roughly hexagonal network is more effective than a random reticulation at releasing stress in the contracting layer. That suggestion has been supported by computer simulations [16], in which, once a roughly 'optimal' polygonal network is attained, it remains fixed from one layer to the next, creating vertical-sided columns.

An analogous geometry appears in other processes of contraction and cracking. In 1922 a British optical engineer named J. W. French observed a kind of mini-Giant's Causeway, on a scale of centimetres, in a dried starch slurry. Stephen Morris and Lucas Goehring have more recently reported the same result (Figure 13), and have verified that an initially rather disordered network of cracks does indeed find approximate geometric order as it descends [17].

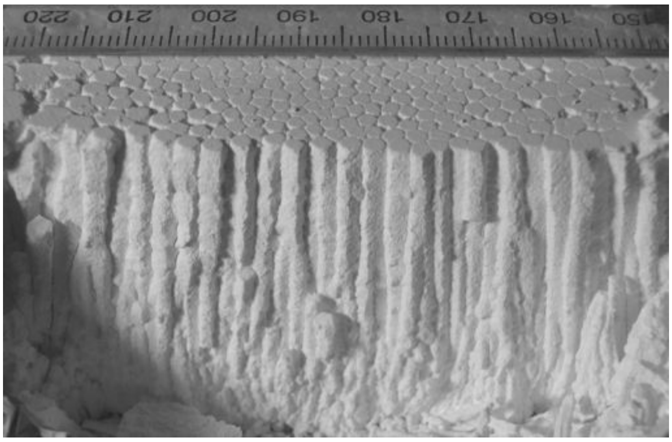


Figure 13   Pseudo-hexagonal columns formed by drying and cracking in a slurry of starch. Image: Stephen Morris, University of Toronto.

Splashes

The second edition of *On Growth and Form* opens with the iconic photograph of a splash formed in milk by a falling droplet (Figure 14), taken by the American electrical engineer Harold Edgerton of the Massachusetts Institute of Technology. In the 1920s Edgerton used the newly invented stroboscope to 'freeze' rapid, repetitive motions when the flash rate of the lamp was synchronized with the cycling rate of the movement. He developed a stroboscopic photographic system that could take 3000 frames per second. The forms and patterns revealed this way in jets of water are captured "live", as it were, in Danish-Icelandic artist Olafur Eliasson's light installation *Model for a Timeless Garden* (2011). These delicate fringed, domed and undulating shapes will be instantly recognized by viewers familiar with *On Growth and Form* [*394-396*].

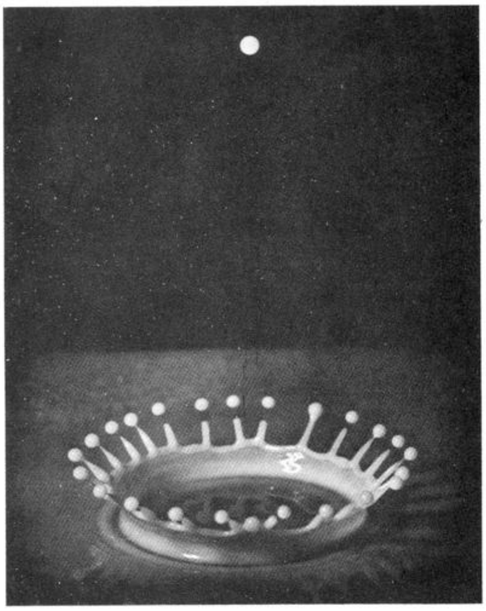


Figure 14 A splash of milk captured by the high-speed photography of Harold Edgerton, forming the opening plate of *OGF*.

Figure 15 *Model for a Timeless Garden* (Olafur Eliasson, 2011).

Edgerton's studies were derived from the high-speed photography of British physicist Arthur Worthington, who also captured the hidden beauty of splashes in the 1870s. Worthington discovered that a splash erupts into a corona that breaks up into evenly spaced jets around its rim, each of them releasing micro-droplets of their own (Figure 16). There is, he said, something seemingly "orderly and inevitable" in these forms, although he admitted that "it taxes the highest mathematical powers" to describe and explain them [18]. Thompson compared Worthington's fluted cup with its "scolloped" and "sinuous" edges to the forms a potter makes at a more leisurely pace from wet clay. He considered this patterning to be analogous to that which created the shapes of soft-tissued living organisms, such as hydroids (marine animals related to jellyfish and sea anemones). Here the form is persistent – yet “there is nothing”, Thompson said, “to prevent a slow and lasting manifestation, in a viscous medium such as a protoplasmic organism, of phenomena which appear and disappear with evanescent rapidity in a more mobile liquid” [*391-2*]. It was, on this occasion, rather too fanciful a speculation.

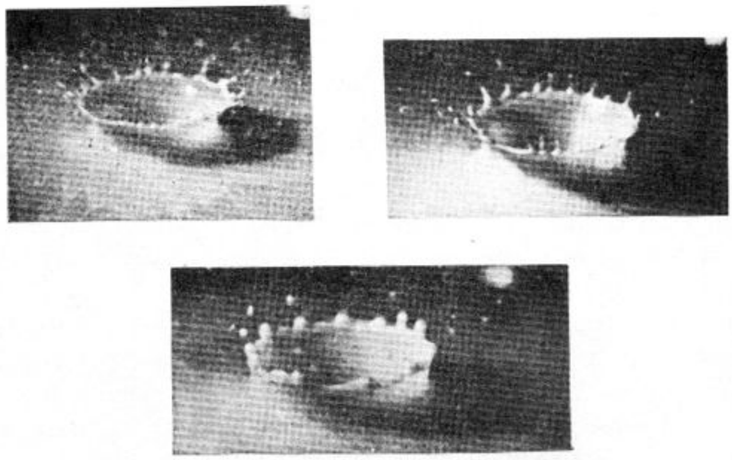


Figure 16 The breakup of a splash, photographed by Arthur Worthington [*389*].

Advances in experimental techniques, coupled to the relevance to practical questions ranging from air-sea gas exchange to the design of inkjet printing, have sustained the formation and breakup of droplets as a topic of contemporary interest in fluid mechanics. Research by Sigurdur Thoroddsen and colleagues, for example, has revealed the extraordinary complexity that can develop in this process [19]. Several hierarchical patterning processes can be involved – for example, the mixing of fluids in the drop and the pool can generate ordered vortices at the interface (Figure 17) [20]. There is, in other words, still unguessed complexity being discovered in the fall of a raindrop.

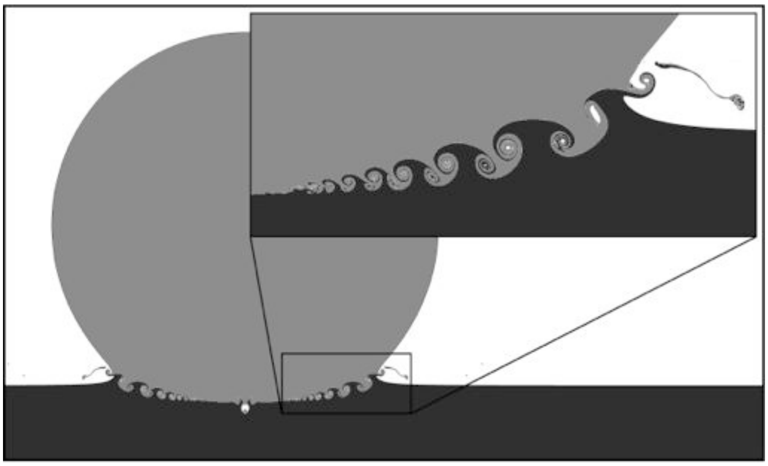


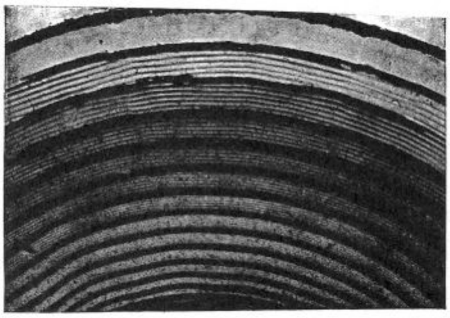
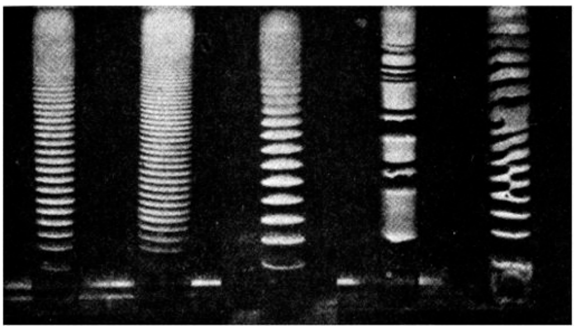
Figure 17 A series of vortices formed at the interface between a droplet and the pool into which it falls, as seen in computer simulations of the process [19]. Image: Sigurdur Thoroddsen and Marie-Jean Thoraval, King Abdullah University of Science and Technology, Saudi Arabia.

Liesegang rings and banded minerals

The sketchiness of some of D'Arcy Thompson's explanations sometimes results not so much from a lack of tools to attack the problem as from an underestimation of the challenge it presents. Such is the case for his discussion of the phenomenon known as Liesegang's rings.

In 1896 the German chemist Raphael Eduard Liesegang discovered that a drop of silver nitrate solution placed on a thin layer of gelatine perfused with potassium bichromate will diffuse through the gel to precipitate a series of concentric rings of reddish brown silver dichromate (Figure 18*a*). The resemblance to the banded structure of agate and onyx was widely noted. Thompson seems rather to wave the mystery away, saying "For a discussion of the *raison d'être* of this phenomenon, the student will consult the textbooks of… chemistry" [*660*]. He is under the impression that the effect has already been explained by Michael Faraday in terms of "the influence on crystallization of the presence of foreign bodies or 'impurities'" [*661*] – in this case, the gelatine itself. Quite how such impurities, presumably randomly distributed, give rise to a periodic banding is not specified.

Thompson goes on to point out that, if Liesegang's reaction is conducted not in a thin film but in a vertical tube of the salt-infused gelatine, with the silver nitrate diffusing from the top later, the result is a series of regular bands (Figure 18*b*). He remarks with a hint of skepticism that some investigators "have been inclined to carry the same chemico-physical phenomenon a very long way" [*663-4*], attributing to some similar effect "the striped leaves of many plants (such as *Eulalia japonica*), the striped or clouded colouring of many feathers or of a cat's skin [and] the patterns of many fishes" [*664*].

a  *b* 

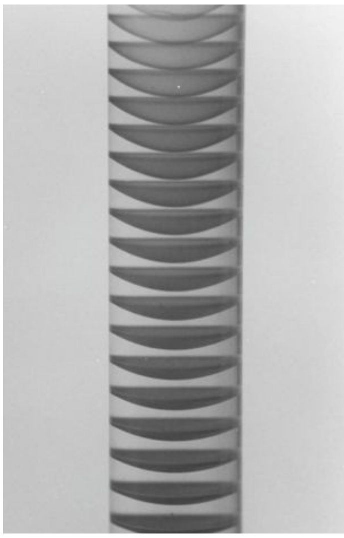
c 

Figure 18   Liesegang rings and bands, as shown in *OGF* (*a*: [*660*]; *b*, [*661*]) and in a modern experiment (*c*) [20]. Image *c*: Rabih Sultan, American University of Beirut, Lebanon.

Unlikely as it might seem, such speculations turn out to carry some force. Liesegang's rings and bands are now known to be an example of a reaction-diffusion chemical process, akin to that postulated by Alan Turing to explain animal markings (see above). They are, however, of a somewhat different variety, for the patterns are here not stationary, constantly maintained dynamic structures in space but are frozen signatures of a pulsed reaction that is periodic in time. They are examples of chemical travelling waves.

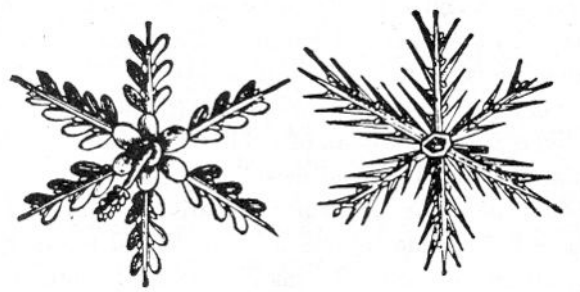
These waves may appear in a reaction-diffusion system under slightly different circumstances from those considered by Turing, but with the same basic ingredients: chemical reactions involving autocatalytic feedback that generates runaway acceleration of the rate at which the products are formed. The waves arise because of a balance between autocatalysis, leading eventually to exhaustion of the reaction, and diffusion, which replenishes the reagents. This balance gives rise to wavefronts that spread like ripples, at which products are formed, followed by a zone of depletion in their wake. The resulting patterns are expanding concentric and spiral structures (Figure 19). Oscillatory reactions were first identified in the 1950s by Boris Belousov in the Soviet Union, and were firmly established, in the face of much disbelief, by his compatriot Anatoly Zhabotinsky during the following decade. The detailed chemical processes were elucidated over the next two decades [21].

Figure 19 Chemical waves in the Belousov-Zhabotinsky reaction. Image: Stephen Morris, University of Toronto.

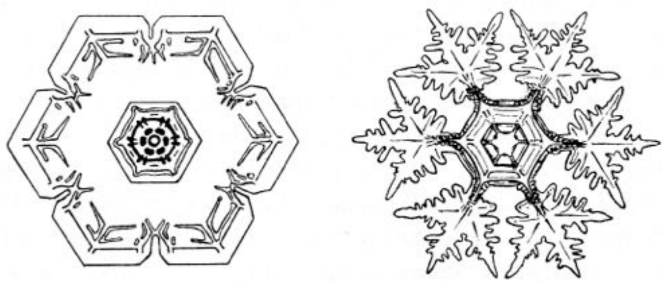
Liesegang's patterns are a variation of this phenomenon in which chemical reaction of the reagents precipitates an insoluble material. Much of the underlying chemistry was, however, already understood by the end of the nineteenth century, thanks in large part to the physical chemist Wilhelm Ostwald, an expert on crystal precipitation and growth. He explained that small crystal 'seeds' cannot grow into a genuine precipitate of silver chromate particles until they surpass a certain critical size. This growth is slowed by the gel, which lowers the rate at which the ions diffuse towards a 'seed'. So the gel gets over-concentrated (supersaturated) in silver chromate, until finally a threshold is crossed and the concentration is high enough to trigger crystal formation (nucleation) everywhere. Then almost all the silver chromate is flushed out in a pulse, producing a band of precipitate, and the concentration remaining in solution falls below the threshold. It takes some time for this concentration to build up again, by which time the diffusion front has moved on. So there is a cycle of supersaturation, nucleation, precipitation and depletion that depoits a train of bands in the wake of the advancing front. This picture captures the essence of the phenomenon, but some of the details – such as the reason for the gradually widening gap between bands – are still being debated [22].

Snowflakes

It is not hard to imagine that Thompson must have been immensely dissatisfied to have been forced to treat in so perfunctory a manner one of the most striking and beautiful manifestations of complex form in nature: the snowflake (Figure 20) [23]. "Crystals lie outside the province of this book", he admitted, "yet snow-crystals, and all the rest besides, have much to teach us about the variety, the beauty and the very nature of form" [*696*]. He was forced again to fall back on sheer description. At first allying snowflakes with all other crystals in displaying geometric symmetry (here hexagonality), Thompson then alludes to what makes these pointed, branches and tenuous flakes so different to the compact, blocky facets of most crystals: "Ringing her changes on this fundamental form, Nature superadds to the primary hexagon endless combinations of similar plates or prisms, all with identical angles but varying lengths of side" [*696*]. Thompson rightly intimated that the hexagonality is the result of the symmetry of the underlying crystal lattice of ice, in which water molecules are arranged in hexagonal rings: "These snow-crystals seem… to give visible proof of the space-lattice on which their structure is formed" [*696*]. But it is in this 'superaddition' that the puzzle lies – why all this seemingly frivolous decoration? Thompson gives no clue.



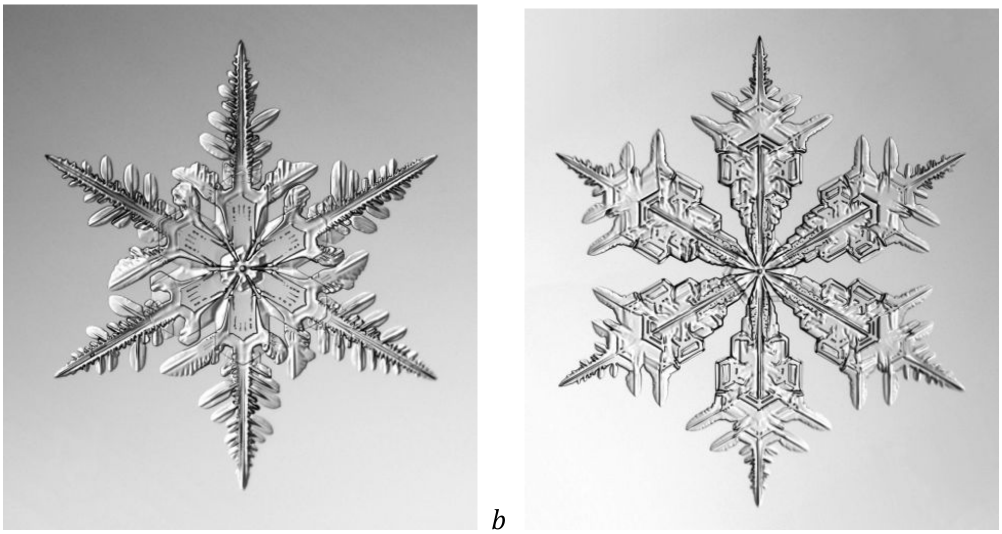
a



b

Figure 20 Snowflakes in *OGF*: as sketched by Dominic Cassini in the seventeenth century (*a*) and as depicted in drawings based on the microphotographs of Bentley and Humphreys [23] (*b*) [*696*].

The truth is that the snowflake combines a representation of the underlying equilibrium geometry of its fabric – the atomic-scale structure of ice – with that of the dynamic process of its growth. The branches result from feedback as the ice crystal grows in moist air. Tiny bumps and irregularities on the ice surface become amplified because they more effectively radiate the latent heat released when water vapour freezes to ice, making them increasingly pronounced [24]. These growth instabilities are random, but they have hexagonality imposed on them from the underlying lattice [25]. The result can be quasi-regular, with branches bearing only an approximate relationship to one another (Figure 21*a*), or it can be highly symmetrical, each branched arm mirroring all the others with astonishing fidelity (Figure 21*b*). Such equivalence of snowflake arms was noted by Thompson, but quite how one arm knows what the others are doing remains a mystery [26] – yet another question of growth and form awaiting an answer.



a *b*

Figure 21 Some snowflakes have arms that are only qualitatively similar (*a*), while for others every arm is identical to the others (*b*). Images: Kenneth Libbrecht, California Institute of Technology, Pasadena.

References

1. D'A. W. Thompson, *On Growth and Form*, 2nd edn. Cambridge University Press, 1942. Reprinted by Dover, New York, 1992.

2. A. Turing, "The chemical basis of morphogenesis." *Phil. Trans. R. Soc. B* **237**, 37-72 (1952).

3. J. D. Murray, *Mathematical Biology*. Springer, Berlin, 1990.

4. H. Meinhardt, *Models of Biological Pattern Formation*. Academic Press, London, 1982.

5. H. Meinhardt, P. Prusinkiewicz & D. R. Fowler, *The Algorithmic Beauty of Sea Shells*. Springer, Berlin, 2003.

6. H. Bénard, "Les tourbillons cellulaires dans une nappe liquide." *Rev. génér. Des Sci.* **12**, 1261-1271 (1900).

7. Lord Rayleigh, "On convection currents in a horizontal layer of fluid, when the higher temperature is on the under side". *Phil. Mag.* **32**, 529-546 (1916).

8. W. Hofmeister, "Allgemeine Morphologie der Gewächse", in *Handbuch der Physiologischen Botanik*, Band 1, Abteilung 2, 405–664. Engelmann, Leipzig, 1868.

9. A. H. Church. *On the Relation of Phyllotaxis to Mechanical Laws.* Williams & Norgate, London, 1904.

10. H. Vogel, "A better way to construct the sunflower head." *Math. Biosci.* **44**, 179–189 (1979).

11. S. Douady & Y. Couder. "Phyllotaxis as a physical self-organized growth process." *Phys. Rev. Lett.* **68**, 2098-2101 (1992).

12. S. Lau, I. de Smet, M. Kolb, H. Meinhardt & G. Jürgens, "Auxin triggers a genetic switch", *Nature Cell Biol.* **13**, 611-615 (2011).

13. R. P. Bhalerao & M. J. Bennett, "The case for morphogens in plants." *Nature Cell Biol.* **5**, 939-943 (2003).

14. A. M. Turing, "Morphogen theory of phyllotaxis", in *Morphogenesis: Collected Works of A. M. Turing,* Vol. 3, ed. P. T. Saunders. North-Holland, Amsterdam, 1992.

15. J. Banks, quoted in W. Guthrie & J. Ferguson (eds), *A New Geographical, Historical, and Commercial Grammar; and Present State of the Several Kingdoms of the World*, 155. G. G. & J. Robinson, London, 1801.

16. E. A. Jagla & A. G. Rojo, "Sequential fragmentation: the origin of columnar quasihexagonal patterns." *Phys. Rev. E* 65, 026203 (2002).

17. L. Goehring, S. W. Morris & Z. Lin, "An experimental investigation of the scaling of columnar joints." *Phys. Rev. E* **74**, 036115 (2006).

18. A. M. Worthington, *A Study of Splashes*. Longmans, Green & Co., London,1908.

19. S. T. Thoroddsen, T. G. Etoh & K. Takehara, "High-speed imaging of drops and bubbles." *Annu. Rev. Fluid Mech.* **40**, 257-285 (2008).

20. M.-J. Thoraval *et al.*, "Van Kármán vortex street within an impacting drop." *Phys. Rev. Lett.* **108**, 264506 (2012).

21. A. T. Winfree, *When Time Breaks Down*. Princeton University Press, Princeton, 1987.

22. S. Sadek & R. Sultan, "Liesegang patterns in nature: a diverse scenery across the sciences", in *Precipitation Patterns in Reaction-Diffusion Systems*, ed. I. Lagzi. Research Signpost Publications, Trivandrum, 2011.

23. W. A. Bentley & W. J. Humphreys, *Snow Crystals*. McGraw-Hill, New York, 1931.

24. W. W. Mullins & R. F. Sekerka, "Stability of a planar interface during solidification of a dilute binary alloy." *J. Appl. Phys.* **35**, 444-452 (1964).

25. E. Ben-Jacob, N. Goldenfeld, J. S. Langer & G. Schön, "Dynamics of interfacial pattern formation." *Phys. Rev. Lett.* **51**, 1930-1932 (1983).

26. P. Ball, "The joy of six: the growth and form of snow crystals", *Interdisc. Sci. Rev.* **29**, 353-365 (2004).