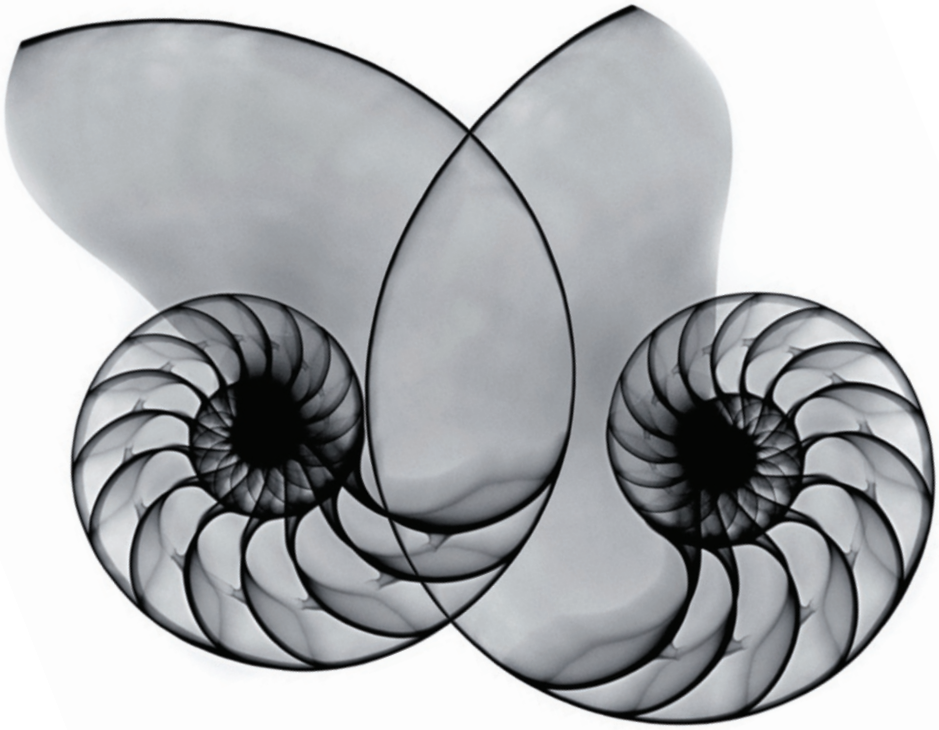

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IN RETROSPECT

On Growth and Form

Philip Ball celebrates a classic work on the mathematics that shape living structures, from antlers to cells.

Like Newton's *Principia*, D'Arcy Wentworth Thompson's *On Growth and Form* is a book more often name-checked than read. Both are hefty — Thompson's revised edition in 1942 weighed in at more than 1,000 pages, to the alarm of Cambridge University Press.

And both books stand apart from their age. Each contains ideas ahead of its time, yet seems rooted in earlier traditions. First published in 1917, with the modern synthesis of neo-Darwinian biology two or three decades away and genes still a nascent concept, *On Growth and Form* looked in some ways archaic by the time the second edition appeared — yet it continues to inspire.

Thompson's agenda is captured in the book's epigraph from statistician Karl Pearson (first published in this journal in 1901): "I believe the day must come when the biologist will — without being a mathematician — not hesitate to use mathematical analysis when he requires it." Thompson presents mathematical principles as a shaping agency that may supersede natural selection, showing how the structures of the living world often echo those in inorganic nature.

On Growth and Form
D'ARCY WENTWORTH THOMPSON
Cambridge University Press: 1917.

Thompson's route to this view was, like the man himself, idiosyncratic. The son of a Cambridge classicist, he went to Edinburgh to study medicine but switched to zoology at Cambridge — the same trajectory as Darwin. There he supplemented his income by teaching Greek. He returned to Scotland as (in effect) a marine biologist at the University of Dundee before moving a few miles down the North Sea coast to the University of St Andrews, where he occupied the Chair of Natural History.

His frustration at the 'Just So' explanations of morphology offered by Darwinians burst out in a 1894 paper presented at the British Association meeting; he argued that physical forces, not heredity, may govern biological form.

On Growth and Form elaborates at length on this theme. "In general no organic forms exist save such as are in conformity with physical and mathematical laws," he wrote. Thompson's demonstration of this claim takes him through a formidable range of topics. To name a few: the mathematical laws that relate growth, flight and locomotion to mass and size (a topic currently experiencing a renaissance); the shapes of cells, bubbles and soap films; geometrical compartmentalization and honeycombs; corals; banded minerals; the intricate shells of molluscs and of the minuscule protozoan radiolarians; antlers and horns; plant shapes; bone microstructure; skeletal mechanics; and the morphological comparison of species.

The book's central motif is the logarithmic spiral, which appears on the plaque commemorating Thompson's former residence in St Andrews. He saw it first in foraminifera, and again in seashells, horns and claws, insect flight paths and the arrangement of leaves in some plants. This, to Thompson, was evidence of the universality of form and the reduction of diverse phenomena to a few mathematical governing principles.

How much influence did *On Growth and Form* have? Evolutionary and developmental biologists often genuflect to Thompson's breadth and imagination while remaining sceptical that he told us much of lasting value.

Thompson was reacting against the Darwinism of his age, whereby, in its first flush of enthusiasm, it seemed adequate to account for every feature with a plea to adaptation. Thompson's insistence that biological form had to make sense in engineering terms was a necessary reminder. But it did not challenge the idea that natural selection was evolution's scalpel — it merely imposed constraints on the forms that might emerge. When he sent the manuscript of *On Growth and Form* to his publisher, Thompson wrote: "where it undoubtedly runs counter to conventional Darwinism, I do not rub this in, but leave the reader to draw the obvious moral for himself."

Thompson believed that evolution could sometimes advance in a leap rather than a shuffle — still a hotly discussed issue. And the debate that Thompson tried to initiate about contingency versus necessity in biological form has not yet really been engaged. There are still biologists who believe that almost every feature of an organism must be adaptive. There are still open questions about how deterministic the course of evolution is.

This is one reason to keep *On Growth and Form* in the canon. Another is the modern appreciation of self-organization as a means of developing complex form and pattern from simple physical rules — evident, for example, in fractal patterns, animal swarming and perhaps even the subtle regularities of human society. Here Thompson is not as easy to enlist as a prophet as one might expect.

Many of the systems he looked at, such as the striped markings of animals, and the formation of polygonal crack networks, are now recognized as paradigmatic examples of spontaneous self-organization in complex systems. But Thompson often gives

such things only a glancing mention while either confessing that he has no real explanation or assuming that it must be a simple one. He says of the chemical precipitation patterns called Liesegang rings, "For a discussion of the *raison d'être* of this phenomenon, the student will consult the textbooks of physical and colloid chemistry." The student would have found little there in 1917, and some aspects of this chemistry are still being clarified.

The logarithmic spiral was, to Thompson, evidence of the universality of form.

The tradition from which Thompson's great work emerged was rather different from the early interest in complex systems by the likes of Henri Poincaré: it was indebted to the biophysics and biomechanics of anatomists such as Wilhelm His and Wilhelm Roux. It is probably this strand that ties Thompson most securely to the present, for much of cell biology now centres on how the mechanics of cell structures determine the fates, forms and functions of tissues. This undervalued aspect of biophysics is becoming more integrated into the rest of molecular biology, as we come to realize how much mesoscale mechanics modulates gene and protein behaviour.

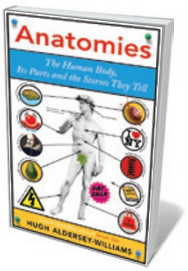
But much of the admiration for *On Growth and Form* expressed by fans such as Peter Medawar and Stephen Jay Gould stems from a more general consideration: Thompson's breadth of scholarship, coupled to the elegance of his writing. He was a classicist as well as a scientist (the many Greek and Latin quotes in *On Growth and Form* pass untranslated), and there is something of the antiquarian in his persona. At a time when science was succumbing to the specialization that has now become something of a liability, Thompson showed the value of synoptic thinkers who are prepared to risk being quite wrong here and there for the sake of an inspirational vision. Like the modern mavericks James Lovelock, Benoit Mandelbrot, Gould and Stephen Wolfram, he presented his ideas in an extended, almost incontinent, gush, rather than with a conventional succession of closely argued papers.

Such figures excite strong responses. They are sometimes exasperating. But we must make sure that they do not — in an age of Big Science, citation-counting, tenure battles and funding crises — become extinct. ■

Philip Ball *is a writer based in London.*
e-mail: p.ball@btinternet.com

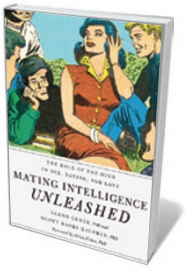
The D'Arcy Thompson Zoology Museum at the University of Dundee, UK, is currently displaying the first works acquired through a grant from the Art Fund to build a collection of art inspired by Thompson's work. A special issue of *Interdisciplinary Science Reviews* on D'Arcy Thompson and his legacy will be published in March 2013.

Books in brief

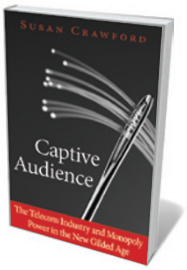


Anatomies: The Human Body, Its Parts and the Stories They Tell
Hugh Aldersey-Williams VIKING *320 pp. £18.99 (2013)*
How comfortable are we with our corporeal selves? Hugh Aldersey-Williams, whose best-seller on the periodic table eulogized the elements, here turns a cultivated eye to the body eclectic, limbs, liver, lungs and all. He roves from Rembrandt's *The Anatomy Lesson of Dr Nicolaes Tulp* (1632) — with its intent crowd of medics round a pallid corpse — to his own observations of cadavers and their nested organs, so distinct in hue, density and texture. A seething melange of science and culture follows: the iconic status of the nose, the shapeliness of kidneys, extreme longevity and much more.

Constant Touch: A Global History of the Mobile Phone
Jon Agar ICON BOOKS *288 pp. £12.99 (2013)*
In this update to his 2003 history of the mobile phone, science and technology historian Jon Agar reassesses the ever-evolving nature of this multitasking machine clamped to the ears of billions. Agar reports on the developments with characteristically clear precision. His four-part chronicle deconstructs a typical mobile phone; traces its genesis and evolution, touching on regional differences; dives into the cultures embracing it, from phone-hacking journalists to African farmers; and, weaving in Apple's part in the story, ends with a bang at the smartphone.



Mating Intelligence Unleashed: The Role of the Mind in Sex, Dating, and Love
Glenn Geher and Scott Barry Kaufman OXFORD UNIVERSITY PRESS *320 pp. $27.95 (2013)*
Human courtship is as convoluted as the human mind. In generating and maintaining relationships we can be master tacticians, deploying everything from humour and compassion to bling and 'bad boy' displays. It is this nexus of intelligence and mating that psychologists Glenn Geher and Scott Barry Kaufman explore in this lively, copiously researched treatise on the roles of factors from creativity to biases and emotional intelligence.



Captive Audience: The Telecom Industry and Monopoly Power in the New Gilded Age
Susan Crawford YALE UNIVERSITY PRESS *256 pp. £20 (2013)*
The United States may be a pioneer of digitization but, says Susan Crawford, it has lost its early lead in broadband pricing and speed — and, in turn, Internet access. In her history-cum-analysis, telecommunications policy specialist Crawford avers that many US citizens pay significantly more than their counterparts elsewhere; and whereas more than half of South Korean households have fast fibre lines, the US figure is just 7%. With monopolies running US cable companies, it is time, she argues, for government regulation.

Blindspot: Hidden Biases of Good People
Mahzarin R. Banaji and Anthony G. Greenwald DELACORTE *272 pp. $27 (2013)*
Unconscious biases that guide behaviour act like retinal blindspots — even blindsight, in which people with brain damage can grab an object without consciously seeing it. So say psychologists Mahzarin Banaji and Anthony Greenwald, arguing that such quirks can trump ethical intent owing to adaptations that may have been evolutionarily advantageous. Starting with perceptual mistakes based on habits of thought (mindbugs), they cover psychological self-trickery in depth.