On Growth and Form

On Growth and Form is a book by the Scottish mathematical biologist D 'Arcy Wentworth Thompson (1860 ? 1948) . The book is long ? 793 pages in the first edition of 1917 , 1116 pages in the second edition of 1942 .
The book covers many topics including the effects of scale on the shape of animals and plants , large ones necessarily being relatively thick in shape ; the effects of surface tension in shaping soap films and similar structures such as cells ; the logarithmic spiral as seen in mollusc shells and ruminant horns ; the arrangement of leaves and other plant parts (phyllotaxis) ; and Thompson 's own method of transformations , showing the changes in shape of animal skulls and other structures on a Cartesian grid .
The work is widely admired by biologists , anthropologists and architects among others , but less often read than cited . Peter Medawar explains this as being because it clearly pioneered the use of mathematics in biology , and helped to defeat mystical ideas of vitalism ; but that the book is weakened by Thompson 's failure to understand the role of evolution and evolutionary history in shaping living structures . Philip Ball on the other hand suspects that while Thompson argued for physical mechanisms , his rejection of natural selection bordered on vitalism .

Overview

D 'Arcy Wentworth Thompson 's most famous work , On Growth and Form was written in Dundee , mostly in 1915 , but publication was put off until 1917 because of the delays of wartime and Thompson 's many late alterations to the text . The central theme of the book is that biologists of its author 's day overemphasized evolution as the fundamental determinant of the form and structure of living organisms , and underemphasized the roles of physical laws and mechanics . At a time when vitalism was still being considered as a biological theory , he advocated structuralism as an alternative to natural selection in governing the form of species , with the smallest hint of vitalism as the unseen driving force .
Thompson had previously criticized Darwinism in his paper Some Difficulties of Darwinism . On Growth and Form explained in detail why he believed Darwinism to be an inadequate explanation for the origin of new species . He did not reject natural selection , but regarded it as secondary to physical influences on biological form .
Using a mass of examples , Thompson pointed out correlations between biological forms and mechanical phenomena . He showed the similarity in the forms of jellyfish and the forms of drops of liquid falling into viscous fluid , and between the internal supporting structures in the hollow bones of birds and well @-@ known engineering truss designs . He described phyllotaxis (numerical relationships between spiral structures in plants) and its relationship to the Fibonacci sequence .
Perhaps the most famous part of the book is Chapter 17 , " The Comparison of Related Forms , " where Thompson explored the degree to which differences in the forms of related animals could be described , in work inspired by the German engraver Albrecht Dürer (1471 ? 1528) , by mathematical transformations .
The book is descriptive rather than experimental science : Thompson did not articulate his insights in the form of hypotheses that can be tested . He was aware of this , saying that " This book of mine has little need of preface , for indeed it is ' all preface ' from beginning to end . "

Editions

The first edition appeared in 1917 with 793 pages , published by Cambridge University Press . The second , enlarged edition appeared in 1942 , with 1116 pages ; it extended many of the chapters somewhat but did not significantly change Thompson 's thesis . Since then it has been reprinted and abridged many times , including in 1943 , 1944 , 1945 , 1948 , 1951 , 1952 , 1959 , 1961 , 1963 , 1966 , 1967 , 1968 , 1969 , 1971 , 1972 , 1973 , 1977 , 1979 , 1980 , 1981 , 1983 , 1984 , 1986 , 1987 , 1988 , 1990 , 1992 , 1994 , 1995 , 1997 , 1999 , 2000 , 2003 , 2004 , 2006 , 2007 , 2008 , 2009 , 2010 , 2011 and 2014 . It has thus been in print continuously since the Second World War . The book has been translated into German , Spanish , French , and Greek . The 1961 edition , skilfully abridged down to 346 pages by John Tyler Bonner , presents the essence of Thompson 's argument .

Contents

The contents of the chapters in the first edition are summarized below . All but Chapter 11 have the same titles in the second edition , but many are longer , as indicated by the page numbering of the start of each chapter . Bonner 's abridgment shortened all the chapters , and removed some completely , again as indicated at the start of each chapter 's entry below .

1 . Introductory

(1st edition p1 - 2nd edition p1 - Bonner p1)
Thompson names the progress of chemistry towards Kant 's goal of a mathematical science able to explain reactions by molecular mechanics , and points out that zoology has been slow to look to mathematics . He agrees that zoologists rightly seek for reasons in animals ' adaptations , and reminds readers of the related but far older philosophical search for teleology , explanation by some Aristotelian final cause . His analysis of " growth and form " will try to show how these can be explained with ordinary physical laws .

2 . On Magnitude

(1st p16 - 2nd p22 - Bonner p15)
Thompson begins by showing that an animal 's surface and volume (or weight) increase with the square and cube of its length , respectively , and deducing simple rules for how bodies will change with size . He shows in a few short equations that the speed of a fish or ship rises with the square root of its length . He then derives the slightly more complex scaling laws for birds or aircraft in flight . He shows that an organism thousands of times smaller than a bacterium is essentially impossible .

3 . The Rate of Growth

(1st p50 - 2nd p78 - Bonner removed)
Thompson points out that all changes of form are phenomena of growth . He analyses growth curves for man , noting rapid growth before birth and again in the teens ; and then curves for other animals . In plants , growth is often in pulses , as in Spirogyra , peaks at a specific temperature , and below that value roughly doubles every 10 degrees Celsius . Tree growth varies cyclically with season (less strongly in evergreens) , preserving a record of historic climates . Tadpole tails regenerate rapidly at first , slowing exponentially .

4 . On the Internal Form and Structure of the Cell

(1st p156 - 2nd p286 - Bonner removed)
Thompson argues for the need to study cells with physical methods , as morphology alone had little explanatory value . He notes that in mitosis the dividing cells look like iron filings between the poles of a magnet , in other words like a force field .

5 . The Forms of Cells

(1st p201 - 2nd p346 - Bonner p49)
He considers the forces such as surface tension acting on cells , and Plateau 's experiments on soap films . He illustrates the way a splash breaks into droplets and compares this to the shapes of

Campanularian zoophytes (Hydrozoa) . He looks at the flask @-@ like shapes of single @-@ celled organisms such as species of Vorticella , considering teleological and physical explanations of their having minimal areas ; and at the hanging drop shapes of some Foraminifera such as Lagena . He argues that the cells of trypanosomes are similarly shaped by surface tension .

= = = 6 . A Note on Adsorption = = =

(1st p277 - 2nd p444 - Bonner removed)
Thompson notes that surface tension in living cells is reduced by substances resembling oils and soaps ; where the concentrations of these vary locally , the shapes of cells are affected . In the green alga Pleurocarpus (Zygnematales) , potassium is concentrated near growing points in the cell .

= = = 7 . The Forms of Tissues , or Cell @-@ aggregates = = =

(1st p293 - 2nd p465 - Bonner p88)
Thompson observes that in multicellular organisms , cells influence each other 's shapes with triangles of forces . He analyses parenchyma and the cells in a frog 's egg as soap films , and considers the symmetries bubbles meeting at points and edges . He compares the shapes of living and fossil corals such as Cyathophyllum and Comoseris , and the hexagonal structure of honeycomb , to such soap bubble structures .

= = = 8 . The same (continued) = = =

(1st p346 - 2nd p566 - Bonner merged with previous chapter)
Thompson considers the laws governing the shapes of cells , at least in simple cases such as the fine hairs (a cell thick) in the rhizoids of mosses . He analyses the geometry of cells in a frog 's egg when it has divided into 4 , 8 and even 64 cells . He shows that uniform growth can lead to unequal cell sizes , and argues that the way cells divide is driven by the shape of the dividing structure (and not vice versa) .

= = = 9 . On Concretions , Spicules , and Spicular Skeletons = = =

(1st p411 - 2nd p645 - Bonner p132)
Thompson considers the skeletal structures of diatoms , radiolarians , foraminifera and sponges , many of which contain hard spicules with geometric shapes . He notes that these structures form outside living cells , so that physical forces must be involved .

= = = 10 . A Parenthetic Note on Geodetics = = =

(1st p488 - 2nd p741 - Bonner removed)
Thompson applies the use of the geodetic line , " the shortest distance between two points on the surface of a solid of revolution " , to the spiral thickening of plant cell walls and other cases .

= = = 11 . The Logarithmic Spiral [' The Equiangular Spiral ' in 2nd Ed .] = = =

(1st p493 - 2nd p748 - Bonner p172)
Thompson observes that there are many spirals in nature , from the horns of ruminants to the shells of molluscs ; other spirals are found among the florets of the sunflower . He notes that the mathematics of these are similar but the biology differs . He describes the spiral of Archimedes before moving on to the logarithmic spiral , which has the property of never changing its shape : it is equiangular and is continually self @-@ similar . Shells as diverse as Haliotis , Triton , Terebra and Nautilus (illustrated with a halved shell and a radiograph) have this property ; different shapes are

generated by sweeping out curves (or arbitrary shapes) by rotation , and if desired also by moving downwards . Thompson analyses both living molluscs and fossils such as ammonites .

= = = 12 . The Spiral Shells of the Foraminifera = = =

(1st p587 - 2nd p850 - Bonner merged with previous chapter)
Thompson analyses diverse forms of minute spiral shells of the foraminifera , many of which are logarithmic , others irregular , in a manner similar to the previous chapter .

= = = 13 . The Shapes of Horns , and of Teeth or Tusks : with A Note on Torsion = = =

(1st p612 - 2nd p874 - Bonner p202)
Thompson considers the three types of horn that occur in quadrupeds : the keratin horn of the rhinoceros ; the paired horns of sheep or goats ; and the bony antlers of deer .
In a note on torsion , Thompson mentions Charles Darwin 's treatment of climbing plants which often spiral around a support , noting that Darwin also observed that the spiralling stems were themselves twisted . Thompson disagrees with Darwin 's teleological explanation , that the twisting makes the stems stiffer in the same way as the twisting of a rope ; Thompson 's view is that the mechanical adhesion of the climbing stem to the support sets up a system of forces which act as a ' couple ' offset from the centre of the stem , making it twist .

= = = 14 . On Leaf @-@ arrangement , or Phyllotaxis = = =

(1st p635 - 2nd p912 - Bonner removed)
Thompson analyses phyllotaxis , the arrangement of plant parts around an axis . He notes that such parts include leaves around a stem ; fir cones made of scales ; sunflower florets forming an elaborate crisscrossing pattern of different spirals (parastichies) . He recognises their beauty but dismisses any mystical notions ; instead he remarks that
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 , and which spiral patterns are by no means " subjective " .
The numbers that result from such spiral arrangements are the Fibonacci sequence of ratios 1 / 2 , 2 / 3 , 3 @.@ 5 ... converging on 0 @.@ 61803 ... , the golden ratio which is
beloved of the circle @-@ squarer , and of all those who seek to find , and then to penetrate , the secrets of the Great Pyramid . It is deep @-@ set in Pythagorean as well as in Euclidean geometry .

= = = 15 . On the Shapes of Eggs , and of certain other Hollow Structures = = =

(1st p652 - 2nd p934 - Bonner removed)
Eggs are what Thompson calls simple solids of revolution , varying from the nearly spherical eggs of owls through more typical ovoid eggs like chickens , to the markedly pointed eggs of cliff @-@ nesting birds like the guillemot . He shows that the shape of the egg favours its movement along the oviduct , a gentle pressure on the trailing end sufficing to push it forwards . Similarly , sea urchin shells have teardrop shapes , such as would be taken up by a flexible bag of liquid .

= = = 16 . On Form and Mechanical Efficiency = = =

(1st p670 - 2nd p958 - Bonner p221)
Thompson criticizes talk of adaptation by coloration in animals for presumed purposes of crypsis , warning and mimicry (referring readers to E. B. Poulton 's The Colours of Animals , and more sceptically to Abbott Thayer 's Concealing @-@ coloration in the Animal Kingdom) . He considers the mechanical engineering of bone to be a far more definite case . He compares the strength of

bone and wood to materials such as steel and cast iron ; illustrates the " cancellous " structure of the bone of the human femur with thin trabeculae which formed " nothing more nor less than a diagram of the lines of stress ... in the loaded structure " , and compares the femur to the head of a building crane . He similarly compares the cantilevered backbone of a quadruped or dinosaur to the girder structure of the Forth Railway Bridge .

= = = 17 . On the Theory of Transformations , or the Comparison of Related Forms = = =

(1st p719 - 2nd p1026 - Bonner p268)
Inspired by the work of Albrecht Dürer , Thompson explores how the forms of organisms and their parts , whether leaves , the bones of the foot , human faces or the body shapes of copepods , crabs or fish , can be explained by geometrical transformations . For example :
Among the fishes we discover a great variety of deformations , some of them of a very simple kind , while others are more striking and more unexpected . A comparatively simple case , involving a simple shear , is illustrated by Figs . 373 and 374 . Fig . 373 represents , within Cartesian co @-@ ordinates , a certain little oceanic fish known as Argyropelecus olfersi . Fig . 374 represents precisely the same outline , transferred to a system of oblique co @-@ ordinates whose axes are inclined at an angle of 70 ° ; but this is now (as far as can be seen on the scale of the drawing) a very good figure of an allied fish , assigned to a different genus , under the name of Sternoptyx diaphana . Thompson 1917 , pages 748 ? 749
In similar style he transforms the shape of the carapace of the crab Geryon variously to that of Corystes by a simple shear mapping , and to Scyramathia , Paralomis , Lupa , and Chorinus (Pisinae) by stretching the top or bottom of the grid sideways . The same process changes Crocodilus porosus to Crocodilus americanus and Notosuchus terrestris ; relates the hip @-@ bones of fossil reptiles and birds such as Archaeopteryx and Apatornis ; the skulls of various fossil horses , and even the skulls of a horse and a rabbit . A human skull is stretched into those of the chimpanzee and baboon , and with " the mode of deformation .. on different lines " (page 773) , of a dog .

= = = Epilogue = = =

(1st p778 - 2nd p1093 - Bonner p326)
In the brief epilogue , Thompson writes that he will have succeeded " if I have been able to shew [the morphologist] that a certain mathematical aspect of morphology ... is ... complementary to his descriptive task , and helpful , nay essential , to his proper study and comprehension of Form . " More lyrically , he writes that " For the harmony of the world is made manifest in Form and Number , and the heart and soul and all the poetry of Natural Philosophy are embodied in the concept of mathematical beauty " and quotes Isaiah 40 : 12 on measuring out the waters and heavens and the dust of the earth . He ends with a paragraph praising the French entomologist Jean @-@ Henri Fabre who " being of the same blood and marrow with Plato and Pythagoras , saw in Number ' la clef de voute ' [the key to the vault (of the universe)] and found in it ' le comment et le pourquoi des choses ' [the how and the why of things] " .

= = Reception = =

= = = Contemporary = = =

" J.P.McM " , reviewing the book in Science in 1917 , wrote that " the book is one of the strongest documents in support of the mechanistic view of life that has yet been put forth " , contrasting this with " vitalism " . The reviewer was interested in the " discussion of the physical factors determining the size of organisms , especially interesting being the consideration of the conditions which may determine the minimum size " .

J. W. Buchanan , reviewing the second edition in Physiological Zoology in 1943 , described it as " an imposing extension of his earlier attempt to formulate a geometry of Growth and Form " and " beautifully written " , but warned that " the reading will not be easy " and that " A vast store of literature has here been assembled and assimilated " . Buchanan summarizes the book , and notes that Chapter 17 " seems to the reviewer to contain the essence of the long and more or less leisurely thesis ... The chapter is devoted to comparison of related forms , largely by the method of co @-@ ordinates . Fundamental differences in these forms are thus revealed " , and Buchanan concludes that the large " gaps " indicate that Darwin 's endless series of continuous variations is not substantiated . But he does have some criticisms : Thompson should have referenced the effects of hormones on growth ; and the relation of molecular configuration and form ; genetics is barely mentioned , and experimental embryology and regeneration [despite Thompson 's analysis of the latter] are overlooked . The mathematics used consists of statistics and geometry , while thermodynamics is " largely absent " .

Edmund Mayer , reviewing the second edition in The Anatomical Record in 1943 , noted that the " scope of the book and the general approach to the problems dealt with have remained unchanged , but considerable additions have been made and large parts have been recast " . He was impressed at the extent to which Thompson had kept up with developments in many sciences , though he thought the mentions of quantum theory and Heisenberg uncertainly unwise .

George C. Williams , reviewing the 1942 edition and Bonner 's abridged edition for the Quarterly Review of Biology (of which he was the editor) , writes that the book is " a work widely praised , but seldom used . It contains neither original insights that have formed a basis for later advances nor instructive fallacies that have stimulated fruitful attack . This seeming paradox is brilliantly discussed by P. B. Medawar [in] Pluto 's Republic . " Williams then attempts a " gross simplification " of Medawar 's evaluation :

It was a compelling demonstration of how readily one can use physical and geometric principles in trying to understand biology . This was a major contribution in 1917 when vitalism was still being defended by prominent biologists . The battle was as won as it is ever likely to be by the time of the 1942 edition . The book was deficient because of Thompson 's lack of understanding of evolution and antipathy for any concepts of historical causation . "

= = = Modern = = =

The architects Philip Beesley and Sarah Bonnemaison write that Thompson 's book at once became a classic " for its exploration of natural geometries in the dynamics of growth and physical processes . " They note the " extraordinary optimism " in the book , its vision of the world as " a symphony of harmonious forces " , and its huge range , including :

the laws governing the dimension of organisms and their growth , the statics and dynamics at work in cells and tissues including the phenomena of geometrical packing , membranes under tension , symmetries , and cell division ; as well as the engineering and geodesics of skeletons in simple organisms .

Beesley and Bonnemaison observe that Thompson saw form " as a product of dynamic forces .. shaped by flows of energy and stages of growth . " They praise his " eloquent writing and exquisite illustrations " which have provided inspiration for artists and architects as well as scientists .

The statistician Cosma Shalizi writes that the book " has haunted all discussion of these matters ever since . "

Shalizi states that Thompson 's goal is to show that biology follows inevitably from physics , and to a degree also from chemistry . He argues that when Thompson says " the form of an object is a ' diagram of forces , ' " , Thompson means that we can infer from an object the physical forces that act (or once acted) upon it . Shalizi calls Thompson 's account of the physics of morphogenesis

ingenious , extremely elegant , very convincing and , significantly , aimed at very large features of the organism : the architecture of the skeleton , the curve of horns or shells , the outline of the organism as a whole .

Shalizi notes Thompson 's simplicity , explaining the processes of life " using little that a second

@-@ year physics undergrad wouldn 't know . (Thompson 's anti @-@ reductionist admirers seldom put it this way .) " . He notes that Thompson deliberately avoided invoking natural selection as an explanation , and left history , whether of species or of an individual 's life , out of his account . He quotes Thompson 's " A snow @-@ crystal is the same today as when the first snows fell " : adding " so , too , the basic forces acting upon organisms " , and comments that we have forgotten other early twentieth century scientists who scorned evolution . In contrast , he argues ,

Thompson owes his continuing influence to the fact that his alternative doesn 't beg questions at every turn . (Also , of course , he wrote beautifully , better than the poets of his day .)

The anthropologist Barry Bogin writes that Thompson 's book

is a tour de force combining the classical approaches of natural philosophy and geometry with modern biology and mathematics to understand the growth , form , and evolution of plants and animals .

Bogin observes that Thompson originated the use of transformational grids to measure growth in two dimensions , but that without modern computers the method was tedious to apply and was not often used . Even so , the book stimulated and lent intellectual validity to the new field of growth and development research .

Peter Coates recalls that

Peter Medawar famously called On Growth and Form " beyond comparison the finest work of literature in all the annals of science that have been recorded in the English tongue . "

Coates argues however that the book goes far beyond expressing knowledge elegantly and influentially , in a form " that can be read for pleasure by scientists and nonscientists " ; it is in his view

one of the most peculiar and original works of modern science , advancing an idiosyncratic view of how organisms develop , a view that was deeply at odds with the intellectual climate of Thompson 's time ... and a textbook on how to think in any field .

The science writer Philip Ball observes that

Like Newton 's Principia , D ? Arcy Thompson 's On Growth and Form is a book more often cited than read . "

Ball quotes the 2nd Edition 's epigraph by the statistician Karl Pearson : " I believe the day must come when the biologist will ? without being a mathematician ? not hesitate to use mathematical analysis when he requires it . " Ball argues that 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 " , and notes his " frustration at the ' Just So ' explanations of morphology offered by Darwinians . " Instead , Ball argues , Thompson elaborates on how not heredity but physical forces govern biological form . Ball suggests that " The book 's central motif is the logarithmic spiral " , evidence in Thompson 's eyes of the universality of form and the reduction of many phenomena to a few principles of mathematics .

The philosopher of biology Michael Ruse wrote that Thompson " had little time for natural selection . " Instead , Thompson emphasised " the formal aspects of organisms " , trying to make a case for self @-@ organization through normal physical and chemical processes . Ruse notes that , following Aristotle , Thompson used as an example the morphology of jellyfish , which he explained entirely mechanically with the physics of a heavy liquid falling through a lighter liquid , avoiding natural selection as an explanation . Ruse is not sure whether Thompson believed he was actually breaking with " mechanism " , in other words adopting a vitalist (ghost in the machine) view of the world . In Ruse 's opinion , Thompson can be interpreted as arguing that " we can have completely mechanical explanations of the living world " ? with the important proviso that Thompson apparently felt there was no need for natural selection . Ruse at once adds that " people like Darwin and Dawkins undoubtedly would disagree " ; they would insist that

the adaptive complexity that we see in the living world simply cannot be explained by physics and chemistry . If D 'Arcy Thompson thought otherwise , it can only be because in some way he was putting special direction into his physical models . He may not have been an explicit vitalist , but there is certainly the odor of spirit forces about what he claims .

Influence

For his revised On Growth and Form , Thompson was awarded the Daniel Giraud Elliot Medal from the United States National Academy of Sciences in 1942 .

On Growth and Form has inspired thinkers including biologists Julian Huxley and Conrad Hal Waddington , mathematician Alan Turing and anthropologist Claude Lévi @-@ Strauss . The book has powerfully influenced architecture and has long been a set text on architecture courses .

On Growth and Form has inspired artists including Henry Moore , Richard Hamilton and Jackson Pollock . In 2011 the University of Dundee was awarded a £ 100 @,@ 000 grant by The Art Fund to build a collection of art inspired by his ideas and collections , much of which is displayed in the D 'Arcy Thompson Zoology Museum in Dundee .