On Growth and Form (1917), by Sir D'Arcy Thompson [1]

By: Ulett, Mark A. Keywords: Forms [2]

Of Sir D'Arcy Thompson's nearly 300 publications, the theoretical treatise *On Growth and Form* [3], first published in 1917, remains the principal work for which he is remembered. This substantial book is still in print today, and merited an editorial review and introductory essays by two important twentieth century biologists, John Tyler Bonner [4] and Stephen Jay Gould [5]. *Growth and Form* was immediately well-received for both its literary style and its scientific significance, as discussed by the biologist Sir Peter Medawar [6]. Despite being almost continuously in print since its first publication, the exact influence of *Growth and Form* on the biological sciences, although widely acknowledged, is yet difficult to characterize. In this work Thompson aimed to unite physics and biology through an analysis of the physical limitations to the growth and structure of organisms. For developmental biologists in particular, Thompson's theory on the transformation of biological forms, presented in the final chapter of *Growth and Form*, was thought provoking.

Thompson outlines his motivation for writing this book in the "Introductory" chapter of *Growth and Form*. As he saw it, unlike physiologists, zoologists and morphologists had not applied a mathematical or physical perspective to their science. Put another way, the science of biological growth and form was not understood mathematically. Here he joined a long list of scientists who sought to answer what was, according to Joseph Needham [7] and others, the central problem of biology: the problem of form. Most early-twentieth century biologists applied experimental methods in their studies of growth and form, that is, they analyzed specific, tractable aspects of the problem. Conversely, Thompson approached this subject with the aim of generalizing the underlying mathematical and physical characteristics of biological form. Thompson was not looking solely at specific examples; rather he sought to discuss the principles of growth and form important across the whole biological realm. His argument was based on the premise that growth and form are inextricably intertwined; one aspect cannot be (adequately) explained without referring to the other. Even though Thompson recognizes that many strictly biological processes influence both the growth and form of organisms, he limits his discussion to the determination [8] and explanation of purely physical influences.

The organization [9] of *Growth and Form* reflects Thompson's overall approach to the problem of form. He begins with a discussion of microscopic forms, such as diatoms and cells, and subsequent chapters focus on increasingly large biological structures. Thompson argues that, in some cases, larger forms can be best understood as products of the accumulation of smaller forms. Despite its focus on physical properties, *Growth and Form* is not a work of reductionist biology, whereby biological structures are explained as merely the product of chemical or physical processes. An example of Thompson's non-reductionist analysis can be seen in his focus on the mathematical independence of larger structures, such as the shapes of teeth (chapter eight) or the spiral of the nautilus' shell (chapter eleven).

An example of Thompson's approach can be seen in the second chapter, "On Magnitude," which begins with an elementary mathematical discussion of spatial magnitude, in which he formulates the simplest correlations between physical forms in mathematical terms with specific examples providing illumination. These correlations include length and weight; surface area and volume; force and area; the relationship between velocity, work and resistance; and many others.

These correlations become explanatory tools in chapter three, "On Growth." Here, Thompson introduces temporal change to his considerations of growth and form. His discussion of numerous mathematical generalizations of growth in various species (or groups of species) lead Thompson to conclude that what he calls "laws of growth" tend to apply to both the individual organism and the species as a whole. Put another way, this means that the growth of an individual organism can be generalized to all of the individuals within a species, or a group of species. This premise allows Thompson to discuss and generalize about the process of morphological growth within certain types of animals, validly grounded on observations of a few organisms. It is on this premise that the generalized "laws of growth" are explicable. Thompson's laws of growth apply to all biological growth, but are expressed in particular ways depending on the environment and organism.

The final chapter, entitled "On the Theory of Transformations, or The Theory of Related Forms" has been of considerable interest to developmental and evolutionary biologists, and it is certainly the most commented-on section of *Growth and Form*. Here Thompson turns to comparative morphology [10], going beyond an analysis of biological form in terms of physics. By drawing morphological examples on a Cartesian coordinate grid, Thompson illustrates the transformation of biological forms as a product of the bending, tilting, or deformation of the grid. For some biologists, this theory might be considered nothing more than an interesting perspective from which to discuss the morphological differences between members in a related group. Conversely, Thompson viewed the deformations of the ordinate grids as representative of significant alterations in various forces or rates of growth throughout the developmental processes of these altered members. As such, it is not the coordinate grid itself that causes the transformation; rather, the grid provides a novel way to visualize the morphological differences between related species.

Growth and Form went through two extensive editorial revisions after its publication in 1917. Thompson undertook the first revision during the Second World War, expanding the original edition from 793 to 1116 pages. (The mention of chapters above conforms to the 1942 edition.) This version was reprinted several times, until in 1961 John Tyler Bonner [4] undertook the difficult task of producing an abbreviated version of a manageable size and for a general audience. The third edition (at a slim 346 pages) represents the core of Thompson's thesis. Also, this latest edition includes brief annotations at the beginning of each of the nine chapters.

The mathematical and physical approach to biological growth and form that Thompson presented in *Growth and Form* was at the time relatively new yet also a return to more classical ways of thinking. For instance, Stephen Jay Gould [5] argues that Thompson was significantly influenced not only by Aristotle [11]'s descriptive approach to biology but also by the more abstract mathematical ideas of Pythagoras and Plato. The influence of these latter two on Thompson's position is clear through his constant focus on the importance of concrete numbers over statistical fluctuations. As Gould puts it, Thompson was a Greek mathematician working with twentieth century materials.

Determining the precise impact of *Growth and Form* on the biological sciences is difficult for several reasons. First, Thompson's book did not inspire a group of followers, as did the work of other mathematical biologists such as Ronald Fisher [12] and John Burdon Sanderson Haldane. Second, this work was not adopted by experimental biologists. Third, Thompson's approach to understanding form stems from a unique perspective, with roots in classics and mathematics. In the mid-twentieth century, when biologists were most actively reading Thompson's book, fewer biologists were being trained in either of these disciplines. Thus, despite numerous commendations arguing for the profound significance of Thompson's achievement in *Growth and Form*, elaborated on in Ruth D'Arcy Thompson's biography of her father, the practical influence of this work on the biological sciences as a whole remains unclear. It seems to have largely been an inspirational rather than a practical influence.

The evidence for the broad importance of this work to numerous fields within biology can be seen in the diverse topics addressed in the volume of collected papers entitled *Growth and Form: Essays Presented To D'Arcy Thompson*. These essays cover a range of topics and were explicitly motivated by the wider picture that Thompson presented in his "masterpiece." Of specific interest for the developmental biologist are the essays by philosopher Joseph Woodger [13] "On Biological Transformations" and Peter Medawar [6] "Size, Shape, and Age." Though these works progress in quite separate directions, their topics and approaches are clearly inspired by Thompson's. Similarly, Julian Huxley's work on allometric growth [14] was, according to John Tyler Bonner [4], quite specifically influenced by *Growth and Form*. More recently, the work of the paleontologist and evolutionist Gould was greatly inspired by Thompson's perspective. One of Gould's first essays focused on Thompson's *Growth and Form*, and Thompson's influence is explicit at almost every point of Gould's career, especially in his acclaimed *Ontogeny and Phylogeny* [15] and lengthy *Structure of Evolutionary Theory* [16], as Claudine Cohen discusses in detail.

Published at a time when mathematics in biology implied statistics, *Growth and Form* presents D'Arcy Thompson's independent vision for a new scientific perspective on biological form. This work remains widely read and an inspiration to audiences both inside and outside the biological sciences. Whereas many early-twentieth-century biologists focused on uncovering the minutiae of molecular biology or arguing the merits of various evidences for evolution [17], Thompson took an alternative approach. He did not attempt to describe the ultimate cause of morphological form. Rather, he limited his discussion to the influence of a wide range of physical phenomena on biological growth and form.

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