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THEMATIC ISSUE ARTICLE: D'ARCY THOMPSON'S CONCEPTUAL LEGACY

"A Single and Indivisible Principle of Unity": *On Growth and Form* in Context

Matthew Jarron[1]

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Abstract
D'Arcy Thompson's *On Growth and Form* is one of the key works at the intersection of science and the imagination. This introductory essay explores the book and its context, drawing on archival sources to provide a unique perspective. It looks at Thompson's own life and career, his experiences at University College, Dundee, and how he came to write the book. It describes the contents of the 1917 first edition (as many today are familiar only with the 1961 abridgement of the 1942 second edition). It looks at the book's initial reception, exploring the context of biological ideas of the time, particularly in regard to Thompson's perceived opposition to Darwinian theory and the debate between vitalism and mechanism. It explores the early influence of the book on ecologists and systems theorists and other early attempts at mathematical biology, as well as its significant influence on artists and architects. It then describes the development of the second edition of the book and the subsequent increase of interest in his work from both artists and scientists. It concludes by summarizing recent initiatives in the D'Arcy Thompson Zoology Museum.

Keywords History of biology · Interdisciplinarity · Mathematical biology · D'Arcy Thompson

Introduction[1]

> *The search for differences or essential contrasts between the phenomena of organic and inorganic, of animate and inanimate things has occupied many men's minds, while the search for community of principles, or essential similitudes, has been followed by few….*
>
> (Thompson 1917, p. 7)

D'Arcy Thompson's *On Growth and Form* is one of the key works at the intersection of science and the imagination. Hailed as "the greatest work of prose in twentieth century science" (Gould 1992, p. ix) it is a book that has inspired scientists, artists, and thinkers as diverse as Alan Turing, C. H. Waddington, Claude Lévi Strauss, Jackson Pollock, and Mies van der Rohe. It pioneered the science of mathematical biology, and its influence in art, architecture, anthropology, geography, philosophy, and many other fields continues to this day. This article is intended as a wide-ranging introduction to this thematic issue of the journal, exploring D'Arcy Thompson's conceptual legacy. It aims to reveal more about *On Growth and Form* by exploring its origins, content, and reception; its place within Thompson's wider career; and some of the many influences it has had. While any one of these topics would be deserving of more in-depth study, there is a distinct value in taking this broad approach to explore the book's rich content, which draws on centuries of past knowledge while also looking to new areas of research in the future. Throughout, the article makes use of original archival sources, principally Thompson's own correspondence, to provide a unique insight into both the development of his ideas and his extensive network of contacts.

1 This article combines a version of an essay published in Jarron (2017) with additional material presented by the author at the conference "Process, Life, Reality. Investigating Dynamic Modes of Being" at the University of Dundee in 2018.

✉ Matthew Jarron
m.h.jarron@dundee.ac.uk

1 Museum Services, University of Dundee, Dundee, Scotland, UK

Early Life

D'Arcy Wentworth Thompson was born in Edinburgh, Scotland, in 1860. His father (also named D'Arcy Thompson) was a teacher and the author of *Day-Dreams of a Schoolmaster*, a book in which he expressed his liberal and forward-looking views on education, his dislike of corporal punishment, and his advocacy of equal education for both sexes. He also was a classicist and became professor of Greek at Queen's College, Galway.

The young D'Arcy inherited his love of classics (and particularly Aristotle) from his father, whereas his passion for natural history was inspired by his grandfather (Joseph Gamgee, a veterinary surgeon) and one of his early teachers (Buckham Hugh Hossack). He was encouraged by the geologist Charles Peach to join the Edinburgh Naturalists' Field Club, and it was to them in 1876 that he gave his first public lecture on Foraminifera, unicellular marine organisms that would continue to fascinate him later in life. Attending the Edinburgh Academy, Thompson found himself in good company—three of his fellow pupils (John Scott Haldane, Diarmid Noel Paton, and William Abbott Herdman) later joined him as Fellows of the Royal Society.

Thompson entered the University of Edinburgh in 1878, intending to pursue a medical degree. One of his tutors was the marine zoologist Charles Wyville Thomson, and Thompson was given the opportunity to research specimens collected by him on the celebrated H.M.S. *Challenger* deep sea expeditions (Corfield 2004). As his interest in biology developed, Thompson decided to give up medicine and pursue a degree in natural science at Cambridge. There he studied zoology under Francis Maitland Balfour and Adam Sedgwick. The Edinburgh-born Balfour (author of an influential textbook on embryology) became a close friend, until his tragic death at the age of 30 while attempting to scale a ridge on Mont Blanc in 1882.[2] After this sudden loss, Thompson and his fellow students were left in the unusual situation of having to teach each other prior to their final examinations. Nevertheless, Thompson graduated with first-class honors in 1883.

One year later, Thompson was given the opportunity to become a university professor at the age of just 24. University College, Dundee, had opened to students in 1883; it was small but eager to expand. In 1884, a chair in biology was founded and awarded to Thompson, although he nearly didn't apply at all after learning that he would have stiff competition from one of the other candidates, a young botanist with a rapidly growing reputation called Patrick Geddes. Another great polymath, Geddes would return to Dundee four years later to occupy a specially endowed chair of botany in Thompson's department, and the two men would become strong allies. Both were committed to an interdisciplinary approach to learning and both were frustrated by the limitations of the required syllabus.

Thompson quickly acquired a reputation as a wide-ranging and increasingly eccentric teacher. One of his successors in Dundee, Alexander Peacock, recalled: "Fortunate were all who saw him use sketches, bits of paper and string, and soap bubbles to explain the mathematics of the honeycomb, the nautilus shell and such like recondite things."[3]

Thompson admired the Germanic universities for pursuing "the idea of Universality of Knowledge" and he was particularly enthused by the cross-disciplinary work being carried out by Hans Przibram and his experimental biology team at the Vienna Vivarium (Coen 2006). Thompson passionately believed in giving students as great a breadth of knowledge as possible, telling them:

> if you dream, as some of you, I doubt not, have a right to dream, of future discoveries and inventions, let me tell you that the fertile field of discovery lies for the most part on those borderlands where one science meets another. There is a cry in the land for specialisation… but depend upon it, that the specialist who is not reinforced by a breadth of knowledge beyond his own specialty is apt very soon to find himself only the highly trained assistant to some other man…. Try also to understand that though the sciences are defined from one another in books, there runs through them all what philosophers used to call the *commune vinculum*, a golden interweaving link, to their mutual support and interpretation. (Thompson 1903, p. 9)

It would be precisely this interweaving link that Thompson would demonstrate so powerfully in his masterpiece, *On Growth and Form*.

The Growth of *On Growth and Form*

With so much work involved in the running of his department, building up an extensive Museum of Zoology in the College, and teaching both day and evening classes, Thompson struggled to find time for his own research. The specimens he was acquiring for the museum provided the inspiration for a series of research papers published in

[2] Esposito (2013) credits Balfour with having introduced Thompson to German biological theory, which would be very influential on his later organicist ideas. However, Thompson was later severely critical of the "the crude morphology and embryology" of Balfour and his contemporaries (D. W. Thompson to E. S. Russell, 29 December 1926, University of St Andrews Library Special Collections, MS 14,329).

[3] MS of B.B.C. lecture broadcast 1 May 1960, University of Dundee Archive Services, URSF 2/12/3(14).

1888–1890 under the title *Studies from the Museum of Zoology*. But only five of the twelve papers were Thompson's work; he was forced to spend far more time helping his students and assistants with their research rather than doing his own.

It was only when Thompson's teaching and administrative load lightened that he was able to commence work on the writing of *On Growth and Form*. Although it was not published until 1917 (his final year in Dundee before moving to the University of St Andrews), Thompson had been thinking about it for many years. As early as 1889 he wrote to one of his students, Mary Lily Walker: "I have taken to Mathematics, and believe I have discovered some unsuspected wonders in regard to the Spirals of the Foraminifera!"[4]

Thompson became increasingly convinced that the laws of mathematics and physics could be used to explain the morphological development of living organisms, but he recognized that this was a controversial idea. One of his assistants, Doris Mackinnon, later recalled that "he had no thought of writing what was in his mind… he would walk up and down the Laboratory thinking his thoughts aloud and discussing his 'heresies' with her" (Thompson 1958).

It was 1908 before Thompson published anything detailed on the topic: a paper in *Nature* on "The Shape of Eggs and the Causes which determine them." In 1911, he raised the subject at the British Association for the Advancement of Science (BA) meeting in Portsmouth, claiming that, "the form of an object is a 'diagram of Forces',– in this sense, at least, that from it we can judge or deduce the forces that are acting or have acted upon it" (Thompson 1911). This powerful visual metaphor, restated in *On Growth and Form*, would become one of his most influential ideas. Also to re-emerge in the book was the content of a paper he gave to the Royal Society of Edinburgh in 1914 on "Mathematics and Morphology," which introduced for the first time his iconic transformation diagrams (Thompson 1915).

Three years before this, as Thompson told his former Dundee assistant W. T. Calman, he had "promised to write a tiny book (at 1/- [1 shilling]) for the Cambridge Press on 'Growth and Form.'"[5] He had been asked by the botanist Albert C. Seward to write a small book on whales for the *Cambridge Manuals of Science and Literature*, but as he told Seward:

> I do not much care about the subject of 'Whales'; I am half afraid of making them talk like little fishes! On the other hand, I have had an idea in my head for a long time of a little book with some such title as 'The Form of Organisms', or 'Growth and Form'. The book would treat, in so far as space and my own powers permitted, of the physical elements in Morphology, the balance of internal and external forces; the cell free and under pressure, the relation of one leaf form to another, the logarithmic spiral of the Snail and of the Ram's horn, the shapes of eggs, some elementary problems of strength, rigidity and locomotion, and so forth. If this subject commends itself to you, I will set to work upon it, but I can only do so at odd moments, and I cannot safely promise you the little book sooner than say six or eight months hence.[6]

The more he considered the subject, however, the larger and more daunting it became; by 1914, little had been done. Indeed, *On Growth and Form* may never have appeared at all had the Great War not reduced Thompson's workload significantly.[7] Writing to his friend Marcus Hartog (professor of zoology at University College, Cork), he noted that the war "has brought me comparative leisure to undertake a very laborious job."[8] Despite the difficulties, he claimed, "I do not repent of undertaking the job, because most of our brother biologists still need to be told that there is such a thing as physical science and that you cannot spin either rope or cobweb without it." He remained convinced that many would view his ideas as those of "a pernicious and dangerous heretic."[9]

Finally in May 1915 Thompson announced to his friend W.R. Sorley: "I have practically finished my book…. It represents some 20 years of work and thought, and I have great hopes that it will be found useful."[10] He sent the draft manuscript to Cambridge University Press, the editor noting that, "the little book on 'Growth and Form' …has now turned out to be a work on a much larger scale."[11] His friend Calman read the draft and suggested that one of the chapters was "longwinded." Thompson replied dolefully: "it gave me the same impression, and so do all the other chapters."[12]

4 Thompson to M. L. Walker, 18 October 1889, University of St Andrews Library Special Collections, MS 44,464.

5 Thompson to W. T. Calman, 4 February 1911, University of St Andrews Library Special Collections, MS 27,387.

6 Thompson to A. C. Seward, 17 December 1910, University of St Andrews Library Special Collections, MS 17,316.

7 In part this was due to the diminished number of students but mostly the temporary cessation of his work as scientific expert at the Fishery Board for Scotland, a post that had placed increasing demands upon his time.

8 Thompson to M. Hartog, 29 January 1916, University of St Andrews Library Special Collections, MS 19,507.

9 Thompson to R. Pearl, 12 June 1917, University of St Andrews Library Special Collections, MS 19,800.

10 Thompson to W. R. Sorley, 17 May 1915, University of St Andrews Library Special Collections, MS 19,393.

11 Cambridge University Press to Thompson, 25 May 1915, University of St Andrews Library Special Collections, MS 42,523.

12 Thompson to Calman, 13 April 1915, University of St Andrews Library Special Collections, MS 27,449.

Partly due to wartime paper shortages and partly due to Thompson's insistence on numerous last-minute changes, *On Growth and Form* was finally published in April 1917. Its content is summarized in the Appendix. Thompson had drawn extensively on the resources available to him in Dundee, including the specimens in his museum and the expertise of his colleagues—particularly the physics professor William Peddie and the engineering professor Thomas Claxton Fidler, both of whom reviewed his text in detail and contributed numerous ideas and illustrations. Doris Mackinnon and one of Thompson's former students, Helen Ogilvie, contributed many more of the book's diagrams. The mathematics professor J. E. A. Steggall and the chemistry professor Alexander McKenzie also assisted. Although not specifically credited, the increasingly far-reaching ideas of Patrick Geddes must also have played a part—by this time Geddes had turned from botany to town planning and was drawing comparisons between cities and biological systems, dealing with issues of growth and form on a much broader level.[13]

The Reception and Context of *On Growth and Form*

The book attracted immediate attention from a wide range of sources. The review in *Nature* stated: "This book, at once substantial and stately, is to the credit of British Science and an achievement for its distinguished author to be proud of. It is like one of Darwin's books, well-considered, patiently wrought-out, learned and cautious—a disclosure of the scientific spirit" (Thomson 1917, p. 21). The comparison to Charles Darwin is interesting, given that many saw the book as opposed to Darwinian evolution. Thompson certainly admired Darwin greatly and managed to persuade the great man to write the preface to the first book Thompson published, a translation of Hermann Müller's *The Fertilisation of Flowers*, published in 1883 shortly after Darwin's death.[14] Thompson also knew and admired Alfred Russel Wallace, who conceived his own theory of evolution by natural selection independently of Darwin. On at least two occasions Wallace visited Thompson in Dundee: "Alfred Russel Wallace was here on Wednesday," Thompson wrote in 1890. "I gave a big Lab[orator]y tea-party in his honour. About 50 or 60 people came; but the dear old Lion would not roar."[15] Evidently he was hoping for some verbal fireworks which failed to ensue.

At the BA meeting in 1894, Thompson gave a paper entitled "Some Difficulties in Darwinism." It was never published, but *Nature* summarized its content:

> He doubts the efficacy of the struggle for existence in the case of humming-birds, &c., and in these cases he regards the profusion of forms, colours, and other modifications as due merely to laws of growth, and thinks that growth may be more exuberant in the absence of struggle and hardship. (Anon 1894, p. 435)

Writing about *On Growth and Form*, Thompson claimed: "I have tried to make it as little contentious as possible. That is to say 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."[16] One of his "morals" was that Darwin was wrong in seeing evolution purely as a slow, gradual process dictated by natural selection. Thompson's Theory of Transformations sought to demonstrate that (according to the second edition) "discontinuous variations are a natural thing, that 'mutations'—or sudden changes, greater or less—are bound to have taken place, and new 'types' to have arisen, now and then" (Thompson 1942, p. 1095).

On Growth and Form appeared at a time of great debate in biological theory, stimulated as much by philosophers of the time as by biologists (Esposito 2013; Nicholson and Gawne 2015; Dresow 2020). As Thompson's friend and colleague Patrick Geddes noted in 1914: "The biological sciences are today, as in the generation of Darwin and [Herbert] Spencer, returning to the foremost line of interest in thought."[17]

For years, much of the debate had been framed around the two opposing views of vitalism and mechanism. In the early years of the 20th century many scientists still held that living organisms were animated by some unexplained "vital force" that was not subject to normal physical laws

[13] By the time Thompson was writing *On Growth and Form*, Geddes was spending much of his time in India so would probably not have been able to comment on drafts of the book. The two remained close, however, and when Thompson left Dundee at the end of 1917, Geddes felt the loss deeply (telling Thompson "now I'll have nobody for a talk at all!") and he also resigned soon after (P. Geddes to Thompson, 8 February 1918, University of St Andrews Library Special Collections, MS 16,422).

[14] It is interesting to note that the publishers also suggested a translation of Wilhelm Focke's *Hybridisation of Flowers*, which Thompson declined. However, Focke's book would later turn out to be highly significant in that it was the only one of its time to pick up on the potential of Gregor Mendel's experiments on plant inheritance. Darwin had been sent a copy of this book, but failed to spot the significance of Mendel's findings, which were not rediscovered until 1900. If Thompson had chosen to translate Focke's book, might he have picked up on the references to Mendel?

[15] Thompson to M. L. Walker, 9 May 1890, University of St Andrews Library Special Collections, MS 44,471.

[16] Thompson to A. E. Shipley, 1915, quoted in Thompson 1958, pp. 161–162.

[17] P. Geddes to Thompson, 22 January 1914, University of St Andrews Library Special Collections, MS 16,428.

(Chen 2018; Donohue and Wolfe 2023). In his Presidential Address to the Zoology Section of the BA in 1911, Thompson claimed that, "The hypothesis of a vital principle, or vital element,… has come into men's mouths as a very real and urgent question, the greatest question for the biologist of all" (Thompson 1911).

The supporters of vitalism included many whose work Thompson admired, notably the German biologist Hans Driesch, author of *Analytic Theory of Organic Development* (1894), whose work Thompson drew on extensively in *On Growth and Form*. The great popular champion of vitalism, however, was the French philosopher Henri Bergson. His 1907 book *Creative Evolution* was widely read, and its English translation in 1911 is likely to have prompted Thompson's BA address. Soon after, he wrote to Geddes, who had recently met Bergson in Paris:

> I envy you your recent trip and especially your talk with Bergson and others. I sent, by the way, a copy of my B.A. Address to Bergson, and got a very kindly note from him in reply.
> Much as I admire what I have read of him, I confess that my admiration is largely directed to his general spirit and tone, and I have difficulty in drawing from him any very clear message, or working hypothesis.[18]

In particular, Bergson's view of the application of mathematics to biology was the polar opposite of Thompson's: "calculation touches, at most, certain phenomena of organic destruction. Organic *creation*, on the contrary, the evolutionary phenomena which properly constitute life, we cannot in any way subject to a mathematical treatment" (Bergson 1911, p. 20).

Thompson's 1911 BA address explored vitalist ideas in some detail, tracing their history from Aristotle and Galen onwards, and his discussion was even used as "a defense of vitalism" by H. V. Neal in the journal *Science* (Neal 1916). Ultimately, however, Thompson concluded by stating: "It is the plain bounden duty of the biologist to pursue his course, unprejudiced by vitalistic hypotheses, along the road of observation and experiment, according to the accepted discipline of the natural and physical sciences" (Thompson 1911, p. 422). He described various recent experiments which "have rather tended to sway a certain number of zoologists in the direction of the mechanical hypothesis."

Thompson's mathematical approach to organic form would seem to place him firmly in this trend towards purely mechanistic thinking. Biologists such as Jacques Loeb were strongly opposed to the vitalist tradition and believed that organisms could be studied in the same way as machines, whose various parts could be entirely explained by physico-chemical processes (Allen 2005).

Similarly, in *On Growth and Form* Thompson states:

> Cell and tissue, shell and bone, leaf and flower, are so many portions of matter, and it is in obedience to the laws of physics that their particles have been moved, moulded and conformed…. Their problems of form are in the first instance mathematical problems, their problems of growth are essentially physical problems, and the morphologist is, *ipso facto*, a student of physical science. (Thompson 1917, p. 7)

However, Thompson was rarely willing to ally himself wholly to the mechanist cause. The one exception was a celebrated debate in 1918 with his old school friend John Scott Haldane and others. Here, Thompson was at his most unequivocal:

> I believe that the material body of a living thing (apart from Consciousness) is a mechanism. I see no other way of investigating in detail its material structure, its form, and its activities. I know no way of studying its material aspects other than by the help of physical and chemical methods, and of the mathematical laws which these sciences rest on in their turn… [19]

Elsewhere, however, Thompson took a slightly different view—he was convinced that, "great as are the lessons of the mechanists, they do not tell the whole story" (Thompson 1919, p. 164). *On Growth and Form* repeatedly makes clear his conviction that the living organism is a system, bound together by an "indissoluble association" (Thompson 1917, p. 713):

> The biologist, as well as the philosopher, learns to recognise that the whole is not merely the sum of its parts. It is this, and much more than this. For it is not a bundle of parts but an organisation of parts, of parts in their mutual arrangement, fitting one with another, in what Aristotle calls 'a single and indivisible principle of unity'; and this is no merely metaphysical conception, but is in biology the fundamental truth…. (Thompson 1917, p. 714).

Such ideas (which would go on to be greatly influential in systems biology) place Thompson as an early advocate of what would come to be known as organicism, a "third way" of biology that rejected the extreme positions of either

[18] Thompson to P. Geddes, 25 October 1911, University of St Andrews Library Special Collections, MS 16,400.

[19] Stated during a debate at a meeting of the Aristotelian Society, 6 July 1918, part of a symposium entitled "Are Physical, Biological and Psychological Categories Irreducible?"

vitalism or mechanism (Esposito 2013; Nicholson and Gawne 2015). It had roots in the ideas of J. S. Haldane and the holism of South African Jan Smuts. In 1929, Thompson participated in a discussion with Haldane and Smuts at the BA meeting in Cape Town, and it may have been partly through Thompson's influence that Smuts later became rector at the University of St Andrews (see also Esposito 2014).

Key to the development of organicist thinking was the mathematician and philosopher Alfred North Whitehead, with whom Thompson had been in correspondence since at least 1906. In 1918, Thompson wrote Whitehead a fascinating letter exploring the nature of three-dimensional space, suggesting that it is only the influence of gravity that restricts our thinking to three dimensions.[20]

Ideas of organicism were particularly appealing to the members of the Theoretical Biology Club in the 1930s, whose leading participants were all admirers of Thompson's work (Peterson 2017). Joseph Needham, for example, corresponded regularly with Thompson, beginning in 1924 when Needham invited him to contribute an article on "The Mechanistic View of Life" to Cambridge University's *Essays on Science and Religion.* After some equivocation, Thompson declined to write the essay, leaving Needham to do it himself—the latter writing "now you will see how much worse it has actually been done than if it had been yours!"[21]

Thompson was particularly supportive of another member of the group, mathematician Dorothy Wrinch. She had attended Thompson's 1918 debate with Haldane and was inspired by that to apply her mathematical skills to biological research, meeting and corresponding regularly with Thompson throughout the rest of his life (Senechal 2021).

The fact that Thompson was asked to contribute to a series called *Essays on Science and Religion* leads us to question what his views on religion were. Although his daughter Ruth claimed that towards the end of his life Thompson's faith grew stronger, as a young man he appeared to hold far more secular ideas. Writing to one of his former students, the religiously zealous Mary Lily Walker, he claimed:

> you and I both know that you are clinging to the old beliefs to wh[ich] all those who love and sorrow cling…. I know, or think I know, that there are only two resurrections in the world; that of the things that sleep in the night and awaken in the day, and that of the things that perish with the winter and live again in the spring. And that the celestial city is the poem of the Universe. And that the only Heaven is in the lifetime of the Good—that Man is immortal, but men perish.[22]

Thompson did, however, share with the vitalists a belief in the human soul and in *On Growth and Form* he wrote:

> It may be that all the laws of energy, and all the properties of matter, and all the chemistry of all the colloids are as powerless to explain the body as they are impotent to comprehend the soul… [C]onsciousness is not explained to my comprehension by all the nerve-paths and neurones of the physiologist; nor do I ask of physics how goodness shines in one man's face, and evil betrays itself in another. (Thompson 1917, p. 8)

Thompson even seems to have flirted briefly with the fashion for spiritualism that was then at a high. In 1890, the secretary of the Society for Psychical Research, Frederic Myers, gave one of the renowned Armitstead Lectures in Dundee, and Thompson chaired the meeting, saying: "Naturalists were ready to admit that beyond the bounds of their own wide province there lay a darker continent that was left for men to explore. Scientists were throwing their light upon that darkness, and were bringing into the realms of science all the phantasms and mysteries and all the accumulated stories and superstitions."[23]

Such hidden mysteries of life were much debated by scientists at the time. Many believed that living, organic matter could be created from nonliving, inorganic material, either (as the Darwinists believed) by gradual evolution or (as many vitalists argued) by some form of spontaneous generation. In 1912, Dundee played host to the annual meeting of the BA, and Thompson was the principal local organizer of the event. Giving the Presidential Address was the renowned physiologist Sir Edward Schäfer, a strong opponent of vitalism, who claimed: "If living matter has been evolved from lifeless in the past, we are justified in accepting the conclusion that its evolution is possible in the present and in the future."[24] Speaking about the development of the cell nucleus, he added, "we may even hope to see the material which composes it prepared synthetically… we may one day be able, by chemistry, to make life."[25]

[20] Thompson to A. N. Whitehead, 20 May 1918, University of St Andrews Library Special Collections, MS 20,371.

[21] J. Needham to Thompson, 5 November 1925, University of St Andrews Library Special Collections, MS 15,482.

[22] Thompson to M. L. Walker, 25 May 1898, University of St Andrews Library Special Collections, MS 44,609.

[23] *Dundee Advertiser*, 22 November 1890. In this Thompson may have been influenced by Alfred Russel Wallace, another enthusiast of spiritualism.

[24] *Dundee Courier*, 5 September 1912.

[25] *The Globe*, 5 September 1912. Schäfer's BA address seems to have had a strong influence on Thompson's attitude to mechanistic thinking, as he told the philosopher W.R. Sorley: "What you say about the Mechanists being less confident than of old was precisely my belief and conviction until Schafer's address, and the reception it got went a

Schäfer believed that the only way to prove this was to re-create under laboratory conditions the missing transitional forms "which we shall be uncertain whether to call animate or inanimate."[26] His comments were reported as sensational in the press, but many scientists had been working in this area for some time. Of greatest interest to Thompson was the French biologist Stéphane Leduc, who spent years generating "artificial organisms" in his laboratory, using salts and silicates to generate an extraordinary variety of lifelike forms (Keller 2002, p. 25). Thompson probably disagreed with Leduc's conclusion that he had found in these creations the fundamental basis or cause of life, but he delighted in finding visual analogies between organic and inorganic forms in order to reveal the ways that both were shaped by the same physical forces.[27] Thompson also enjoyed a productive correspondence with Emil Hatschek, a Hungarian-born chemist based in London who became a recognized expert in the form of colloids, encouraging Thompson's detailed interest in soap bubbles, which he referred to repeatedly in his studies of cell division and aggregation.

In contrast to most scientific works, *On Growth and Form* frequently describes nature in terms of its aesthetic qualities. As discussed later (and see also Jarron 2021), Thompson had a great love of art and undoubtedly found a sense of beauty in the natural patterns he studied. He also particularly enjoyed teaching arts students alongside those studying science, until new Arts Ordinances introduced by the University in 1911 (which he regarded as disastrous) effectively ended such interdisciplinarity, confining his teaching solely to science students. It is unsurprising, therefore, that many of the people whose work helped to shape *On Growth and Form* also brought together art and nature. The famous transformation diagrams are one example, taking as their starting point Albrecht Dürer's work on geometry and proportion in his *Four Books on Human Proportion* (1512–1528). As well as dealing with transformations of the human form, Dürer's work on proportion also encompassed his theories of ideal beauty, claiming that, while beauty was ordered by as-yet undefined laws, it was not an objective concept but based on the infinite variety of nature. Dürer was writing at a time when an increasing emphasis was being placed on empirical observation of the natural world, and for him, as for Thompson, the wonder of nature was not in a single ideal of perfection, but in the existence of multiple variations on natural forms (Anon 2010).

Also fascinated by this infinite variety was Ernst Haeckel, the German biologist whose extraordinary illustrations of Radiolaria in *Art Forms in Nature* (1899–1904) Thompson drew on liberally; indeed, he owned a set of plaster models of Radiolaria based on Haeckel's artworks. Thompson's friend Hans Przibram is another example of a scientist turned artist—his drawings were published in the Vienna Secession's art magazine *Ver Sacrum*. The art critic Theodore Cook was another interesting precursor—his books *Spirals in Nature and Art* (1903) and *The Curves of Life* (1914) contained an admirably wide range of examples, although Thompson dismissed the "mystical conceptions" of those like Cook who saw in the logarithmic spiral "a manifestation of life itself" (Thompson 1942, p. 751).

One could mention many others who helped and inspired Thompson in writing his magnum opus, but it is worth noting that Thompson himself devoted the final paragraph of the book to a eulogy of the French entomologist Jean-Henri Fabre, whose series of popular-science books on insects made him one of the most celebrated scientists of his day. Thompson wrote that Fabre "curiously conjoined the wisdom of antiquity with the learning of today" (Thompson 1917, p. 779), a claim that could easily have been made of Thompson himself. One of the most notable aspects of *On Growth and Form* is the way that Thompson treats the ideas of Aristotle and Galileo with the same significance as the latest scientific research. He also sought to make the natural world accessible to wider audiences, giving many public lectures, radio broadcasts and (in 1918) giving the celebrated Royal Institution Christmas Lectures for children.

From the First Edition to the Second

At the end of the book, Thompson noted: "while I have sought to shew [sic] the naturalist how a few mathematical concepts and dynamical principles may help and guide him, I have tried to shew the mathematician a field for his labour,—a field which few have entered and no man has explored" (Thompson 1917, p. 778). If he was hoping for a rush of eager biomathematicians to start exploring the field, he was to be disappointed. Only a handful of significant works followed over the next two decades, but it is worth mentioning the authors behind these, since all of them had direct connections to Thompson.

In Vienna, Hans Przibram and his brother Karl continued their investigations, many of the results of which were published in *Form and Formula in the Animal Kingdom* (1922). Thompson corresponded regularly with both of them (Hans

long way to prove the contrary" (Thompson to Sorley, 29 April 1913, University of St Andrews Library Special Collections, MS 19,392).

[26] *The Globe*, 5 September 1912.

[27] The references to Leduc in *On Growth and Form* are among the few reminders today of how popular his theories once were. Many eminent biologists supported his idea of synthetic biology (also known as plasmogeny), including Jacques Loeb and Alfonso Herrera, both of whom were correspondents of Thompson.

began one of his letters "Dear and venerated master!")[28] and sent many of his students to work there. He also encouraged other young scientists to visit, notably Joseph Woodger and Dorothy Wrinch, both future members of the Theoretical Biology Club.

In England, the biologist Julian Huxley dedicated his 1932 book *Problems of Relative Growth* to Thompson. They had been corresponding in the mid-1920s, as Huxley became interested in issues of relative growth in fiddler crabs and other organisms. Thompson recognized the value of Huxley's research for his intended revision of *On Growth and Form*, telling him, "I can see that this work of yours is going to improve vastly my Growth-chapter in the next edition."[29]

At the same time, Ronald A. Fisher and J. B. S. Haldane were pioneering the mathematical study of population genetics in a series of influential papers in the 1920s. Haldane was a lifelong acquaintance of Thompson's, being the son of John Scott Haldane, while Fisher's work at the Rothamsted Experimental Station (an agricultural research institute in Hertfordshire) led to Thompson sending students there as well. Thompson was interested in their research (he refers to J. B. S. Haldane's work in the second edition of *On Growth and Form*) but was wary of what he saw as "over-mathematization." Writing to Dorothy Wrinch, he claimed:

> R.A. Fisher is continually guilty of it. I'm really quite ready to admit there are cases, a few cases, where all the refinements of [Fisher and others] may shew their usefulness; but when they will use these sledge-hammer methods when the tack-hammer or the drawing pin would do as well, I've no patience with them. JBS is by no means free from the same bad habit; he just loves to show off his mathematics.[30]

Despite this, Thompson strongly believed in the role of mathematicians in biology. Writing in 1931, he argued: "There are innumerable biological problems with a mathematical bearing; but the mathematics required is mostly of too high an order for the biologist. Nothing is more wanted in biology than that mathematicians of first-class standing should interest themselves in biological problems."[31]

The two researchers whose work in this area Thompson most admired were the Italian Vito Volterra and the Ukrainian-born American Alfred Lotka. Both were interested in population dynamics and independently developed mathematical models for predator-prey relationships and interspecific competition in ecological systems. Thompson regularly promoted the work of both men and went to some lengths to help get Volterra's work published in the UK. "All Volterra's stuff is good," he wrote to Oxford University Press. "It is a real contribution to the theory of Natural Selection."[32] Volterra undoubtedly admired Thompson, telling him: "Your works on biological mathematics are very well known and estimated by us."[33]

Thompson was also impressed by the work of Russian mathematician Vladimir Kostitzin, describing his *Biologie Mathematique* (1937) as "an admirable little book…. It opens our eyes to a variety of biological problems which lie remote from elementary or conventional mathematics, but may nevertheless be brought under mathematical treatment with great advantage" (Thompson 1937, p. 943). When Kostitzin wrote to Thompson, he referred to him as "dear Master."[34]

Arguably the person most committed to developing Thompson's area of study into a new and viable science was Nicolas Rashevsky, another Ukrainian based in the United States. His *Mathematical Biophysics—Physico-Mathematical Foundations of Biology* (1938) began by crediting "the remarkable book, On Growth and Form" (Rashevsky 1938, p. vii). In turn, Thompson reviewed Rashevsky's book for *Nature*, noting that, "it tackles problems which we dearly want to solve, it tries methods which have not been used before, and it leaves us dreaming of possibilities far beyond what are yet actually attained" (Thompson 1938). Rashevsky would go on to found the first university program in mathematical biology, at the University of Chicago, and launch the *Bulletin of Mathematical Biophysics*, still published today as the *Bulletin of Mathematical Biology* (Keller 2002, pp. 82–89). Thompson took some trouble to promote Rashevsky's work in Britain, and they corresponded regularly. Rashevsky frequently called on Thompson's help at various crisis points in his career.[35]

By this time, Thompson had finally started work on a second edition of *On Growth and Form*. It had been on his

[28] H. Przibram to Thompson, 2 November 1935, University of St Andrews Library Special Collections, MS 25,830.

[29] Thompson to J. Huxley, 5 March 1925, University of St Andrews Library Special Collections, MS 28,563.

[30] Thompson to D. Wrinch, 18 March 1943, University of St Andrews Library Special Collections, MS 24,476/9.

[31] Thompson's reference letter for Dorothy Wrinch to University of London, 29 May 1931, University of St Andrews Library Special Collections, MS 24,429.

[32] Thompson to R. W. Chapman, undated, University of St Andrews Library Special Collections, MS 11,370.

[33] V. Volterra to Thompson, 7 July 1926, University of St Andrews Library Special Collections, MS 49,396. See also Israel and Gasca 2002.

[34] V. Kostitzin to Thompson, 28 June 1938, University of St Andrews Library Special Collections, MS 25,785 (translated from French).

[35] For example, N. Rashevsky to Thompson, 30 January 1929 and 27 February 1934, University of St Andrews Library Special Collections, MSS 49,417 & 49,418.

mind since 1923, when the first edition sold out. Writing to Joseph Larmor (professor of mathematics at Cambridge) he explained:

> The Press at first wanted to reprint from the old plates, making merely verbal corrections, and adjusting new matter (where absolutely necessary) in an appendix. Against this I protested; on the ground that, after eight years, very considerable alterations were required; and on the ground also that a really new edition would be likely to sell much better…. Well, after a good long delay, the Press have agreed to let me have a free hand in the matter of alterations and additions.[36]

Another fifteen years would pass before Thompson finally knuckled down to the task and, in 1940, he wrote to his successor in Dundee, Alexander Peacock:

> I have at last, at the long last—finished re-writing Growth and Form. The chapter on Growth itself (chap. III) has been the great stumbling-block, and has been written over and over again. Alas, I may have 'missed the bus'—as the politicians say. I am half afraid to send the MS up to the Cambridge Press lest they tell me there's 'Nothin' doin.'[37]

Even then, it was another two years before the much-expanded second edition finally made it into print. "I wrote this book in wartime," Thompson noted, "and its revision has employed me during another war. It gave me solace and occupation, when service was debarred me by my years" (Thompson 1942, p. iv).

Thompson's revisions consisted mostly of additions—little was removed from the text of the first edition and the same division into seventeen chapters was retained. There were, however, many more illustrations culled from a variety of sources (particularly photographs, reflecting the advances in scientific photography since the first edition); more statistical data (for example, drawn from Julian Huxley's work on fiddler crabs, mentioned above); and more examples to demonstrate existing points (unequal growth in the tail feathers of a humming bird, for example, or the similarity of a vulture's metacarpal bone to a Warren truss). Numerous additional references were added to works published since the first edition, showing that Thompson (though now in his 80s) was keeping up-to-date with biological literature. However, despite the increased page count (over 1100 pages compared to 800 for the first edition) there were few new areas of research. Venation patterns on insect wings and the shape of horses' teeth were among the few new additions to have been studied in depth.

Unsurprisingly, the reviewers this time were far less kind. Writing in *Science*, C. E. McClung complained that, "the entire subject of cytogenetics is left untreated. Surely the significance of all the modern work on this subject must be appreciated, and yet there is no mention of genes and little of chromosomes" (McClung 1942, p. 472).

By this time, Thompson's ideas seemed to have become completely disassociated from biology's increasing focus on evolution and genetics, something of which he was all too often aware. As early as 1916 he had suggested that, "the biologist must face dynamical problems, and not dally with material structures [i.e., genes] to which he ascribes more or less miraculous properties."[38] Seven years later he wrote: "The chromosome people are having a good innings; but their theories are top-heavy, and will tumble down of their own weight. It is of little use, meanwhile, to argue with them."[39]

Thompson is often accused of being ignorant of developments in genetics, but as Maurizio Esposito has noted, his surviving papers contain numerous notes on the subject, evidence of a strong interest (Esposito 2014, p. 99). Nor does he entirely ignore the topic in the second edition of *On Growth and Form*, but simply sets it aside as a separate field of research:

> The efforts to explain 'heredity' by help of 'genes' and chromosomes, which have grown up… since this book was first written, stand by themselves in a category which is all their own and constitutes a science which is justified of itself. To weigh or criticise these explanations would lie outside my purpose, even were I fitted to attempt the task…. I leave this great subject on one side not because I doubt for a moment the facts nor dispute the hypotheses nor decry the importance of one or other. (Thompson 1942, p. 340)

Alexander Peacock later claimed that, "D'Arcy's originality and versatility made him unclassifiable by formal standards and his individualism inhibited his founding of a school for the development of his ideas."[40] But the ideas still lingered, and the second edition of *On Growth and Form* found new

[36] Thompson to J. Larmor, 17 October 1923, University of St Andrews Library Special Collections, MS 41,213.

[37] Thompson to A. D. Peacock, 28 April 1940, University of Dundee Archive Services, URSF 2/12/2(2).

[38] Thompson to M. Hartog, 29 January 1916, University of St Andrews Library Special Collections, MS 19,507. Genes had been identified by Hugo de Vries in 1889, following earlier observations by Gregor Mendel, but were only given the name "gene" in 1909.

[39] Thompson to F. L. Lewis, 13 October 1923, University of St Andrews Library Special Collections, MS 28,584.

[40] A. D. Peacock, MS of B.B.C. lecture broadcast 1 May 1960, University of Dundee Archive Services, URSF 2/12/3(14).

followers, particularly among embryologists—or developmental biologists, as they would come to be known from the late 1950s (MacCord and Maienschein 2021)—and others who recognized that the questions Thompson was asking were important, even if the answers he provided (and the methods he used to obtain them) were not always the right ones.

In 1945, to mark his 60th anniversary as a professor, Wilfred Le Gros Clark and Peter B. Medawar edited a volume of *Essays on Growth and Form* presented to Thompson as a Festschrift. Julian Huxley, J. H. Woodger, and Alfred Lotka were among the contributors. Medawar was a talented young biologist who would go on to win the Nobel Prize for his part in the discovery of acquired immune tolerance. He had corresponded enthusiastically with Thompson since 1942 and later wrote an illuminating postscript to Ruth D'Arcy Thompson's biography of her father, in which he claimed that *On Growth and Form* is "beyond comparison the finest work of literature in all the annals of science that have been recorded in the English tongue" (Thompson 1958, p. 232).[41] The Festschrift was reviewed in *Nature* by Conrad Hal Waddington, a former member of the Theoretical Biology Club whose work on epigenetics owed much to Thompson. Waddington wrote: "there are some whose influence has been so decisive in stimulating the widespread exploration of a scientific problem which they were unequivocally responsible for pointing out, that a tribute to their insight comes spontaneously to the mind of their followers when the occasion arises" (Waddington 1946, p. 87).

One of the most notable thinkers to take inspiration from the second edition of *On Growth and Form* was the father of modern computing, Alan Turing. In the early 1950s Turing turned his attention to biology with his landmark paper, "The Chemical Basis of Morphogenesis" (Turing 1952). This began an investigation into animal patterning that Thompson had briefly introduced at the end of the second edition of *On Growth and Form* with a study of the zebra's stripes. Turing proposed that there were chemicals in the body called morphogens which worked their way to the surface using a mathematical process called reaction-diffusion, thus creating visual patterns such as the zebra's stripes. In 1988, his ideas were taken further by James Murray in his celebrated paper, "How the Leopard Gets its Spots," which used computer simulations to show that the reaction-diffusion model could explain most if not all of the wide variety of animal coat markings found in nature (Murray 1988; see also the similarly titled Goodwin 2001).[42]

The introduction of computers had a profound effect on biology, enabling the use of highly sophisticated mathematical models of the sort that Thompson could never have predicted but would undoubtedly have welcomed. In 1969, C. H. Waddington and R. J. Cowe created the first computer simulation of shell patterning (Waddington and Cowe 1969). Around the same time, Hans Meinhardt began using computer modelling of tissue formation to explain the regenerative capabilities of hydra (Gierer and Meinhardt 1972). One of the first to recognize the implications of this new technology for biology was the paleontologist and evolutionary biologist Stephen Jay Gould, who in 1971 published an influential paper that did much to restore Thompson's reputation (Gould 1971; Dresow 2017). Richard Dawkins later claimed that, "It is one of the minor tragedies of biology that D'Arcy Thompson died just before the computer age, for almost every page of his great book cries out for a computer" (Dawkins 1996, p. 200). Now, finally, Thompson's "field which few have entered and no man has explored" could become a fertile territory for a new generation of researchers, with mathematical biologists or biomathematicians continuing to grow in number today.

The Multidisciplinary Reach of *On Growth and Form*

Thompson's influence has gone far beyond biology. His importance to general systems theory was recognized by two of its key founders, Ludwig von Bertalanffy (who had taught Thompson's ideas to his students at the University of Vienna in the 1930s) and Kenneth Boulding, who considered *On Growth and Form* to be "central to the evolution of his own thinking" (Hammond 2003, p. 34). One of the key elements of early systems theory was cybernetics, and its pioneer, Norbert Wiener, also acknowledged the importance of *On Growth and Form* in his landmark book, *Cybernetics or Control and Communication in the Animal and the Machine* (1948). It also proved an inspiration to the anthropologist Claude Lévi-Strauss, who refers to Thompson in his important book on *Structural Anthropology* (1963). More recently, the growing science of nanochemistry has been acknowledged by one of its pioneers, Geoffrey Ozin, to have important roots in Thompson's work (Ozin and Arsenault 2005). Sara Cannizzaro argues that the emerging field of biosemiotics also owes a significant debt to *On Growth and Form*, exploring what biological morphological

[41] In private, Medawar was more critical about the book, writing, "from a formal point of view, it is unprecise and incomplete;…faulty in many ways biologically" (Medawar to Joseph Needham, 10 July 1942, quoted in Peterson 2017, p. 154).

[42] It was not until 2012 that researchers at King's College London provided the first experimental evidence to confirm Turing and Murray's ideas (Economou et al. 2012).

transformation might teach us about forms of cultural and aesthetic transformation (Cannizzaro 2014).

In architecture and engineering, *On Growth and Form* has inspired creators and practitioners from Le Corbusier and Ove Arup to Norman Foster and Cecil Balmond. Thompson's work on the mechanical efficiency of soap bubbles and the structural tension of dragonfly wings helped to inspire the development of lightweight structures such as Buckminster Fuller's geodesic domes and Frei Otto's Olympic stadium in Munich (Beesley and Bonnemaison 2008). Ludwig Mies van der Rohe, one of the pioneers of modernist architecture, added the book to the reading lists for his students at Illinois Institute of Technology (Lambert 2001). For Jørn Utzon, architect of the Sydney Opera House, *On Growth and Form* was so fundamental to his practice that it was "the only book he specifically recommended new staff to read" (Weston 2002, p. 23). In particular, the idea of organisms constantly subject to transformation through external pressures lies at the root of the theories of emergence, organic architecture, and natural design that form a fundamental part of current architectural theory.

Like architects, artists were much quicker than scientists in recognizing the potential of Thompson's ideas. The sculptor Henry Moore discovered *On Growth and Form* as a student, and its influence can undoubtedly be seen in the series of "Transformation Drawings" that he created in the early 1930s, which use overlapping pencil lines to depict organic forms apparently in the act of morphing from one state to another (Jarron 2015, p. 165). Moore was soon discussing *On Growth and Form* with the influential art critic Herbert Read, who introduced it to the St Ives circle of artists including Paul Nash, Barbara Hepworth, and Naum Gabo. Thompson's work soon found its way to other avant-garde artists, including Laszlo Moholy-Nagy, who was based in Britain during 1935–1937 and referred to Thompson in his posthumously published book *Vision in Motion* (1947).

The second edition of *On Growth and Form* was also enthusiastically taken up by a group of students at the Slade School of Fine Art in London in the 1940s, including Nigel Henderson, Richard Hamilton, Eduardo Paolozzi, and William Turnbull. In 1951, Hamilton staged an influential exhibition called *Growth and Form* at Herbert Read's new Institute of Contemporary Art (ICA). Along with another Thompson enthusiast, Victor Pasmore, Hamilton would go on to become an important teacher at the Department of Fine Art in King's College, Newcastle. The new Basic Design Course they introduced proved to be hugely influential on art schools around the country, and it included exercises based on *On Growth and Form* (Crippa and Williamson 2013). Elsewhere in the world, such celebrated artists as Jackson Pollock and Salvador Dalí are known to have read and drawn on the book (Kemp 2006). Meanwhile, early pioneers of computer art, such as Roy Ascott and Desmond Paul Henry, saw *On Growth and Form* as a key prefigurement of their work, and one can trace a direct line of descent from Thompson through Benoît Mandelbrot's work on fractals to the computer-generated imagery of Pixar and others today.[43]

Thompson himself probably had only a slight realization of the creative impact his work had, although Herbert Read wrote to him towards the end of his life, telling him that, "you have built the bridge between science and art. The danger lies in one's impulse to cross it too impetuously, without a proper understanding of the country on the other side."[44] Thompson was one of the few people who could cross this bridge fearlessly, having a strong interest in art as well as biology and classics. In 1900, Thompson had commissioned the Celtic Revivalist artist George Dutch Davidson to design a series of three decorative panels for his study, the subjects to be Orpheus, Neptune, and Juno, each surrounded by animals. Tragically, Davidson died (aged just 21) before these could be carried out, but Thompson continued to befriend and correspond with artists throughout his life (Jarron 2021). One of the notable features of *On Growth and Form* is the number of artistic analogies that Thompson draws—the book abounds with references to the potter's wheel, the sculptor's clay, and particularly the art of the glassblower, which "is full of lessons for the naturalist as also for the physicist" (Thompson 1917, p. 238).

Today the University of Dundee continues to promote the links between art and science which Thompson demonstrated so forcefully. Although the huge Museum of Zoology that he created was demolished in the 1950s, his surviving collection is now displayed in the D'Arcy Thompson Zoology Museum. Opened in 2008, the museum is used not just in teaching life sciences but also by students of fine art, design, philosophy, creative writing, and other subjects. The museum and Thompson's ideas are also central to a new Master of Fine Arts course in Art, Science and Visual Thinking, introduced at Duncan of Jordanstone College of Art & Design in 2021. In recent years, the museum has also been building its own collection of art inspired by Thompson's ideas and specimens. As well as works by major 20th-century artists such as Moore, Pasmore, and Wilhelmina Barns-Graham, the museum has also acquired pieces by significant contemporary artists, including Will Maclean, Susan Derges, and Peter Randall-Page, and has introduced new artists to Thompson's ideas through residencies and

[43] A notable example of this is Andy Lomas, who created digital effects for *Avatar* and the *Matrix* films while also exhibiting his algorithm-derived art prints in galleries, citing Thompson as a key influence (Jarron 2015, p. 166).

[44] H. Read to Thompson, undated but probably 1944, University of St Andrews Library Special Collections, MS 25,480.

the commissioning of the D'Arcy Thompson Print Folio. Drawing on Dundee's heritage as a major center for comics production, the museum has also published a D'Arcy Thompson comic, introducing his life and ideas in graphic form (Jarron et al. 2017).

In 2017, the museum co-organized a major interdisciplinary conference to celebrate the centenary of *On Growth and Form*.[45] Held in Dundee and St Andrews, it was one of numerous events marking the book's anniversary, which also included conferences, workshops, and discussion events in Amsterdam, Cambridge, Edinburgh, Heidelberg, Leiden, London, Loughborough, Minneapolis, New York, Singapore, and others. These in turn gave rise to special journal editions of *Development*, *The Mathematical Intelligencer*, *Mechanisms of Development*, *Nature*, and now this special issue of *Biological Theory*. All of this demonstrates the ongoing interest in and relevance of Thompson's work, which shows no sign of abating as *On Growth and Form* enters its second century.

Appendix: The Form of *On Growth and Form*

For all its importance, the first edition of *On Growth and Form* is a work that few people today have actually read from cover to cover, and many are likely to be more familiar with the abridged 1961 edition still in print today. It is therefore worth providing a short summary of the book's contents, quoting some of the most evocative passages to give a sense of D'Arcy Thompson's distinctive style. "This little book of mine has little need of preface," Thompson begins, "for indeed it is 'all preface' from beginning to end. I have written it as an easy introduction to the study of organic Form, by methods which are the common-places of physical science… but which nevertheless naturalists are still little accustomed to employ" (Thompson 1917, p. v).

Chapter One ("Introductory") sets out Thompson's mission: "We want to see how, in some cases at least, the forms of living things, and of the parts of living things, can be explained by physical considerations, and to realise that, in general, no organic forms exist save such as are in conformity with ordinary physical laws" (p. 10). This may seem to be stating the obvious but Thompson was keen to ensure that his readers accepted the logic of his increasingly controversial argument. He then goes on to introduce the idea that form is shaped by physical forces: "The form, then, of any portion of matter, whether it be living or dead, and the changes of form that are apparent in its movements and in its growth, may in all cases alike be described as due to the action of force" (p. 11).

Chapter Two ("On Magnitude") looks at relative size, showing how larger organisms such as ourselves are principally affected by gravitational force: "Were the force of gravity to be doubled, our bipedal form would be a failure, and the majority of terrestrial animals would resemble short-legged saurians, or else serpents" (p. 32).[46] By contrast, "the form of smaller organisms is largely independent of gravity, and largely… due to the force of surface-tension" (p. 33). This distinction between larger and smaller forms will "affect the whole course of our argument throughout this book" (p. 34).

Chapter Three concerns "The Rate of Growth," focusing on the effects of unequal growth rates in different parts of the body, particularly in organisms such as tadpoles that go through significant periods of metamorphosis. This is a field which came to be known as allometry and to which Thompson is credited as having made a fundamental contribution (Horder 2018). In this section of the book Thompson was drawing considerably on data gathered by Hans Przibram's team at the Vienna Vivarium, and also the recent popularity of biometry spearheaded by the work of English statistician Karl Pearson.[47]

Chapter Four deals with "The Internal Form and Structure of the Cell." At that time, very little was yet known about the inner workings of cells and Thompson demonstrates some visual analogies between karyokinesis (division of the cell nucleus) and the force lines of a bipolar electrical field. Thompson was much aided in this analysis by his colleague in Dundee, William Peddie, who proposed some of the key ideas, and his Cork friend Marcus Hartog, an expert on karyokinesis.

Chapter Five looks at "The Form of Cells," concentrating on the effects of surface tension on their external form. Thompson uses a variety of visual analogies here, including soap bubbles, sealing wax, drops of oil, splash patterns, and the forms created by blowing glass. This is followed by Chapter Six ("A Note on Adsorption"), a brief addendum to the previous chapter, which concludes that "the agreement of cell-forms with the forms which physical experiment and mathematical theory assign to liquids under the influence of surface tension, is so frequently… manifested, that we are

[45] "On Growth and Form 100," 13–15 October 2017, University of Dundee and University of St Andrews.

[46] In 2014, a team from the University of Bath demonstrated how mechano-morphogenetic processes are coordinated to generate a body shape that withstands gravity, through work on the medaka fish (*Oryzias latipes*). Porazinski et al. (2015).

[47] A strong ally of Thompson's in this area was the American biologist Raymond Pearl, who described *On Growth and Form* as "one of the most important biological books of our time" (Pearl to Thompson, 12 February 1929, University of St Andrews Library Special Collections, MS 19,802). In turn, Thompson told Pearl: "you are among the first half dozen men whom I kept in mind when I was writing the book" (Thompson to Pearl, 12 June 1917, University of St Andrews Library Special Collections, MS 19,800).

led… to accept the surface tension hypothesis as generally applicable and as equivalent to a universal law" (p. 202).

Chapter Seven moves from single cells to "The Forms of Tissues or Cell-Aggregates." Again, Thompson makes extensive use of soap bubbles to show how the principle of minimal surface area forces a change in the shapes of the bubbles as they cluster together. He looks in detail at hexagonal symmetry and its appearance in a wide variety of natural forms, from honeycombs to corals. The same subject is continued in Chapter Eight, looking at the shapes created during egg segmentation and the partitioning of space in corals, leaves, and other forms.

Chapter Nine discusses "Concretions, Spicules, and Spicular Skeletons." In a recurring theme, Thompson compares organic and inorganic forms, for example the spicules of certain corals with those of salt crystals. He goes on to examine the skeletons of simple unicellular organisms such as Foraminifera and Radiolaria. In the former, the skeletal material covers the entire outer surface of the cells and thus they "assume some configuration comparable to that of a fluid drop or of an aggregation of drops" (p. 439). By contrast, Radiolarian skeletons, which Thompson compares to snow crystals, are formed when silica particles accumulate in the regular gaps of the mesh-like frothy protoplasm that covers the organism's surface, gradually becoming more complex but following a number of predetermined patterns. He concludes this part with a very brief chapter about geodetics (now known as geodesics, a geodesic line being the shortest path between two points in a curved space).

Chapter Eleven deals with one of the best-known subjects of *On Growth and Form*, "The Logarithmic Spiral." Thompson explains this as based on a gnomon—a figure which, when added to a given figure, makes a larger figure of the same shape. Thompson looks at various examples of this in shell forms (most famously the nautilus) and explores the related growth patterns that give rise to them (including examples of what would now be called isometric growth).[48] Chapter Twelve continues the same theme, focusing in on the spiral shells of Foraminifera.

Chapter Thirteen takes us on to more complex organisms including mammals and birds, examining "The Shapes of Horns, and of Teeth or Tusks." Among the animals he refers to here are Huia birds, which would have been familiar from his museum collection—he was fortunate to have acquired a pair of these New Zealand birds shortly before they were hunted to extinction. The Huia were unique in that the male and female of the species had differently shaped beaks, but as Thompson demonstrates here, the curve of growth was actually the same in each.

Chapter Fourteen deals with "Leaf-Arrangement, or Phyllotaxis." Here Thompson felt himself on relatively safe ground: "The spiral leaf-order has been regarded by many learned botanists as involving a fundamental law of growth, of the deepest and most far-reaching importance" (p. 635). In particular, Thompson noted that, "as regards the number of the helical or spiral rows, certain numerical coincidences are apt to recur again and again, to the exclusion of others" (p. 638). These numbers are known as the Fibonacci sequence, and although Thompson takes some time to set out the evidence for this, he ultimately concludes that, "its supposed usefulness, and the hypothesis of its introduction into plant-structure through natural selection, are all matters which deserve no place in the plain study of botanical phenomena" (p. 651).[49]

Chapter Fifteen looks at "The Shapes of Eggs, and of Certain Other Hollow Structures." Drawing in part on Thompson's earlier publication on this topic in *Nature*, it also includes an examination of sea urchin morphology, comparing their form to that of liquid drops.

Chapter Sixteen ("On Form and Mechanical Efficiency") is the one that brings Thompson's work most fully into the realm of engineering and bio-design. Here he looks at the forms of larger animals according to their mechanical function and the stresses they are required to endure, arguing that the origins of what were usually seen as functional adaptations arising from evolution could be found instead in physical causes. Most famously, he looks at the forms of quadrupeds (such as horses and dinosaurs), comparing their forms to those of cantilever bridges. Much of this section was supplied to Thompson by his Dundee friend Thomas Claxton Fidler, whose *Practical Treatise on Bridge Construction* (1887) was seen as a definitive text. Thompson showed the similarity between the forms of these animals' skeletons and the diagrams of stresses placed upon them, concluding, "skeletal form, as brought about by growth, is to a very large extent determined by mechanical considerations, and tends to manifest itself as a diagram, or reflected image, of mechanical stress" (p. 712).

The final chapter is perhaps the most famous and radical in the book, presenting Thompson's Theory of Transformations. By applying a Cartesian grid to the form of an organism (or a part of one) and subjecting it to some simple mathematical transformations, he sought to show the similarities of form between related species, in which any

48 This is an area in which considerable work has been done in recent years, and mathematicians can now model a wide variety of shell forms including complex features such as spines and ridges that might seem to be purely ornamental (for example Fowler et al. 1992; Phillips and Brook 2004).

49 In 1993, however, French biomathematicians Stéphane Douady and Yves Couder demonstrated that the recurrence of these numbers is not, as Thompson supposed, a coincidence, but the inevitable consequence of a particular growth pattern (Douady and Couder 1993; Stewart 1998).

differences "might have been brought about by a slight and simple change in the system of forces to which the living and growing organism was exposed" (p. 728).[50] The diagrams that he used to demonstrate this have become the most iconic images of the book. After showing a series of illustrations of fish, Thompson concluded that, "variation has proceeded on definite and orderly lines, that a comprehensive 'law of growth' has pervaded the whole structure in its integrity, and that some more or less simple and recognisable system of forces has been at work" (p. 727).

In the Epilogue, Thompson concludes: "That I am no skilled mathematician I have had little need to confess, but something of the use and beauty of mathematics I think I am able to understand. I know that in the study of material things, number, order and position are the threefold clue to exact knowledge; that these three, in the mathematician's hands, furnish the 'first outlines for a sketch of the Universe'" (p. 778).[51]

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[50] Only after working out this method did Thompson become aware of the work of Italian biologist Giovanni Schiaparelli, who had proposed a similar use of Cartesian planes to transform one form into another in 1898.

[51] Thompson quotes the expression "a sketch of the Universe" from Oliver Goldsmith's *A History of the Earth and Animated Nature* (1774).

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