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“Cell and tissue, shell and bone, leaf and flower” – *On Growth and Form* in Context

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> “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.”[1]

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”[2], 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 biomathematics, and its influence in art, architecture, anthropology, geography, cybernetics and many other fields continues to this day.

D’Arcy Wentworth Thompson was born in Edinburgh, Scotland, in 1860. His father (also named D’Arcy Thompson) was a classics teacher and would eventually become Professor of Greek at Queen’s College, Galway. The young D’Arcy inherited his love of classics from his father, while his passion for natural history was inspired by his grandfather and one of his early teachers. He was encouraged to join the Edinburgh Naturalists’ field club, and it was to them that he gave his first public lecture, on micro-organisms called Foraminifera – a topic that would continue to fascinate him later in life.

D’Arcy 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 D’Arcy was given the opportunity to research specimens collected by him on the celebrated *H.M.S. Challenger* expeditions. As his interest in biology developed, D’Arcy decided to give up medicine and pursue a degree in Natural Science at Cambridge. Here he studied zoology under Francis Maitland Balfour and Adam Sedgwick. The Edinburgh-born Balfour (author of an acclaimed work on *Comparative Embryology*) became a close friend, until his tragic death while attempting to scale a ridge on Mont Blanc. After this sudden loss, D’Arcy and his fellow students were left in the unusual situation of having to teach each other prior to their final examinations. Nevertheless, D’Arcy graduated from Trinity College with First Class Honours in 1883, and remained in Cambridge to take up a position as junior demonstrator in Physiology with Professor Michael Foster, who would also become a close friend and confidante.

Just over a year later, D’Arcy was given the opportunity to become a university professor at the age of just 24. University College in Dundee had opened to students in 1883 with a unique founding principle that it would offer education equally to male and female students. The college was small but eager to expand. In 1884, a chair in Biology was founded and awarded to D’Arcy, although he nearly didn’t apply at all after learning that one of the other candidates was a young botanist called Patrick Geddes, whom he assumed would get the job. Another great interdisciplinarian, Geddes would return to Dundee four years later to occupy a specially endowed chair of Botany in D’Arcy’s department, and the two men would become strong allies.

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[1] D’Arcy Thompson, *On Growth and Form,* 2nd edition (Cambridge University Press, 1942) p1096-7. Referred to as *OG&F* in future references.

[2] Stephen Jay Gould in his introduction to *On Growth and Form* (Canto edition 1992) p ix

Student numbers started small (D'Arcy had just two students in his first class), but quickly began to grow, particularly after the founding of the Medical School in Dundee, which D'Arcy also did much to bring about. He quickly acquired a reputation as a wide-ranging and increasingly eccentric teacher. His successor 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] D'Arcy admired the Germanic universities for pursuing "the idea of Universality of Knowledge" and he particularly admired the interdisciplinary work being carried out by Hans Przibram and his experimental biology team at the Vienna Vivarium. He deplored the fact that in Scotland "our Universities are limited to the teaching of a somewhat meagre array of subjects, of what is obviously necessary, of what will attract what we choose to call a respectable number of students, in a word, of what may be said to pay."[4]

D'Arcy 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... 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.[5]

It would be precisely this interweaving link that D'Arcy would demonstrate so powerfully in his masterpiece *On Growth and Form*. But with so much work involved in the running of his department, building up an extensive museum collection and teaching both day and evening classes, D'Arcy 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 1888-90 under the title *Studies from the Museum of Zoology*, though just five of the twelve papers were D'Arcy's work.

It was only when his teaching and administrative load lightened that D'Arcy 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, D'Arcy had been thinking about it for many years. In 1889 he wrote to one of his students: "I have taken to Mathematics, and believe I have discovered some unsuspected wonders in regard to the Spirals of the Foraminifera!"[6]

D'Arcy became increasingly convinced that the laws of mathematics could be used to explain the growth and form of living organisms. But when he first shared these ideas with others, the response was discouraging. "I confess I am not very much attracted by the line of work, and doubt if it's likely to be very fruitful," his Cambridge mentor Michael Foster wrote in 1894.[7] One of D'Arcy's assistants, Doris

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[3] From MS of BBC lecture broadcast 1/5/1960 (University of Dundee Archive Services, URSF 2/12/3(14))
[4] Address delivered at the opening of session 1903-4, quoted in *The College* December 1903 p9
[5] Address delivered at the opening of session 1903-4, quoted in *The College* December 1903 p9
[6] Letter to Mary Lily Walker 18/10/1889 (University of St Andrews Library Special Collections MS 44464)
[7] Ruth D'Arcy Thompson, *D'Arcy Wentworth Thompson: The Scholar-Naturalist* (Oxford University Press, 1958) p89-90. Referred to as *Scholar-Naturalist* in future references.

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.”[8] It was 1908 before he 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 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”.[9] 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 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.[10]

Finally in 1915 D’Arcy’s various ideas were assembled into book form and he sent it to Cambridge University Press, who noted that “the little book on ‘Growth and Form’ …has now turned out to be a work on a much larger scale”.[11] D’Arcy drew 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 (Peddie’s most notable additions focused on electrical forces in cells, while Fidler supplied the famous diagrams comparing the structure of bridges to the skeletons of dinosaurs and other quadrupeds). Doris Mackinnon and one of D’Arcy’s former students, Helen Ogilvie, contributed many more of the book’s diagrams. Although not specifically credited, the increasingly far-reaching ideas of Patrick Geddes must also have played a part – by this time Geddes had turned to town planning and was drawing comparisons between cities and biological systems, dealing with issues of growth and form on a much broader level.

Partly due to wartime paper shortages and partly due to D’Arcy’s insistence on numerous last-minute changes, *On Growth and Form* was finally published in 1917, attracting 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.”[12] The comparison to Darwin is interesting, given that many saw the book as an opposition to Darwinian evolution. D’Arcy certainly admired Darwin greatly, and managed to persuade him to write the preface to his first publication, a translation of Hermann Müller’s *The Fertilisation of Flowers*, published in 1883 shortly after Darwin’s death. But at the British Association meeting in 1894 D’Arcy gave a paper entitled ‘Some Difficulties in Darwinism’, and he became increasingly convinced that natural selection did not provide all the answers. Writing about *On Growth and Form*, D’Arcy claimed: “I have tried to make it as little contentious as possible. That is to say where it undoubtedly runs counter to

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[8] *Ibid* p161

[9] D’Arcy Thompson, ‘Magnalia Naturae; or The Greater Problems of Biology’, *Science* vol 34 Issue 875, pp 417-428

[10] D’Arcy Thompson, ‘Morphology and Mathematics’, *Transactions of the Royal Society of Edinburgh* vol 50 part 4 no 27 (1915) pp857-895.

[11] Letter to D’Arcy Thompson from Cambridge University Press 25/5/1915 (University of St Andrews Library Special Collections MS 42523)

[12] *Nature* 13/9/1917

conventional Darwinism, I do not rub this in, but leave the reader to draw the obvious moral for himself."[13]

If D'Arcy's work apparently contradicted evolutionary theory, it also contradicted the opposing view of vitalism. In the early years of the twentieth century many scientists still believed that living organisms were animated by some unexplained 'vital force' that was not subject to normal physical laws. This view was held by close friends of D'Arcy's, such as physiologist John Scott Haldane, and many with whom he regularly corresponded, such as Hans Driesch (author of *Analytic Theory of Organic Development* (1894)), on whose work he drew extensively in *On Growth and Form*. In his Presidential Address to the Zoology Section of the British Association in 1911, D'Arcy 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."[14] A key purpose of *On Growth and Form*, however, was to demonstrate that "of the construction and growth and working of the body… physical science is, in my humble opinion, our only teacher and guide."[15]

Related to the concept of vitalism was the commonly held idea of teleology, or 'final cause' in nature. Although D'Arcy was wary of this, noting that "it is but one way, not the whole or the only way"[16], he was evidently much taken by the idea. Inspired, perhaps, by his beloved Aristotle, he saw it as "a common way, and a great way, for it brings with it a glimpse of a great vision, and it lies deep as the love of nature in the hearts of men."[17]

On Growth and Form shows D'Arcy's interests in the aesthetic qualities of the organisms and mathematical patterns he describes, so it is no surprise that many of the people whose work helped to shape *On Growth and Form* also brought together art and nature. They included Ernst Haeckel, the German biologist whose extraordinary illustrations of radiolarians in *Art Forms in Nature* (1899-1904) D'Arcy drew on liberally; indeed, he owned a set of plaster models of radiolarians based on Haeckel's artworks.[18] Another important precursor was the art critic Theodore Cook, whose books *Spirals in Nature and Art* (1903) and *The Curves of Life* (1914) contained an admirably wide range of examples, although D'Arcy dismissed the "mystical conceptions" of those like Cook who saw in the logarithmic spiral of the nautilus shell "a manifestation of life itself",[19] and bluntly dismissed the notion that the sequence of numbers dictating it converged on the Golden Mean as "a mathematical coincidence devoid of biological significance".[20]

Also of interest is D'Arcy's friendship with the Danish artist and palaeontologist Gerhard Heilmann. Having abandoned his medical studies to become a professional artist, Heilmann's series of papers on the origin of birds (1913-16) were dismissed by the biological establishment in Denmark but found an enthusiastic welcome from D'Arcy, who described them as "beautiful and original"[21] and began a

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[13] *Scholar-Naturalist* p161-2
[14] D'Arcy Thompson, 'Magnalia Naturae; or The Greater Problems of Biology', *Science* vol 34 Issue 875, pp 417-428
[15] *OG&F* p13
[16] *OG&F* p6
[17] *OG&F* p4
[18] Three of these models are still held in the D'Arcy Thompson Zoology Museum, University of Dundee
[19] *OG&F* p751
[20] *OG&F* p931
[21] *OG&F* p1080

correspondence which led to Heilmann contributing several of the celebrated transformation diagrams in *On Growth and Form*.

One could mention many others who helped and inspired D'Arcy in writing his *magnum opus*, but it is worth noting that D'Arcy 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. D'Arcy wrote that Fabre "curiously conjoined the wisdom of antiquity with the learning of today", a claim that could easily have been made of D'Arcy himself.[22] One of the most notable aspects of *On Growth and Form* is the way that D'Arcy treats the ideas of Aristotle and Galileo with the same significance as the latest scientific research.

At the end of the book, D'Arcy noted: "while I have sought to shew 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."[23] 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, perhaps the most notable being Julian Huxley's *Problems of Relative Growth* (1932) that was dedicated to D'Arcy. By that time, he had started work on a second edition of *On Growth and Form*, but it was not completed until 1942. "I wrote this book in wartime," he noted, "and its revision has employed me during another war. It gave me solace and occupation, when service was debarred me by my years."[24] This time the reviewers were less kind. Writing in *Science*, C E McClung complained that "the entire subject of cytogeneties 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."[25]

By this time, D'Arcy's ideas seemed to have become completely disassociated from biology's increasing focus on evolution and genetics. Peacock 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."[26] But the ideas lingered and found new followers – perhaps most notably Alan Turing. the father of modern computing..

On Growth and Form shows how complex biological systems can be understood by fundamental mathematical principles, and as such D'Arcy's ideas provided an important basis for the development of modern systems theory. Turing's experimental thinking machines rely on similar ideas, and in the early 1950s Turing turned his attention to biology with his landmark paper 'The Chemical Basis of Morphogenesis'.[27] This began an investigation into animal patterning that D'Arcy had briefly introduced at the end of the second edition of *On Growth and Form* with a study of the zebra's stripes (one of many regrettable omissions from the current abridged edition). Turing's work demonstrated how a mathematical model called reaction-diffusion applied to chemicals in the body that he called morphogens could

[22] *OG&F* p1097
[23] *OG&F* p1096
[24] *OG&F* p iv
[25] C E McClung, 'Growth and Form, *Science* vol 96 no 2499 (1942) p472.
[26] From MS of BBC lecture broadcast 1/5/1960 (University of Dundee Archive Services, URSF 2/12/3(14))
[27] Alan Turing, 'The Chemical Basis of Morphogenesis', *Philosophical Transactions of the Royal Society*, B, 237 (1952) pp37-72

create visual patterns such as this. In 1988 his ideas were taken further by James Murray in his celebrated paper ‘How the Leopard Gets its Spots’, which used computer modelling to show that reaction-diffusion could explain most if not all of the wide variety of animal coat markings found in nature.[28]

D’Arcy had been all too aware of the limits of the mathematics of the time to undertake the task he had begun, admitting: “The organic forms which we can define, more or less precisely, in mathematical terms… are of many kinds, as we have seen; but nevertheless they are few in number compared with Nature’s all but infinite variety.”[29] The introduction of computers had a profound effect on biology, enabling the use of highly sophisticated mathematical models of the sort that D’Arcy could never have predicted but would undoubtedly have welcomed. Stephen Jay Gould was the first to recognise the implications of this and in 1971 published an influential paper that did much to restore D’Arcy’s reputation.[30] 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.”[31] Now, finally, the evolutionists and geneticists who had hitherto dismissed D’Arcy’s work looked at it with fresh eyes and since then the “all but infinite variety” of nature has been increasingly mapped and understood in mathematical terms. Pedro Miramontes of the National Autonomous University of Mexico, one of the many institutions around the world now specialising in biomathematics, recently stated that D’Arcy “simply will be the most influential character in the future of biology.”[32]

D’Arcy’s influence has gone far beyond biology. His importance to systems theory was also recognised by Norbert Wiener, the pioneer of cybernetics, acknowledged 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 Levi-Strauss, who refers to D’Arcy 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 D’Arcy’s work.[33] Within geography, the book has also proved a significant influence, for example in the algorithms used to create the Worldmapper series of cartograms in 2007, a way of visualising data on world poverty and health using D’Arcy’s transformation diagrams as their starting point.

In architecture and engineering, *On Growth and Form* has inspired creators and practitioners from Le Corbusier and Mies van der Rohe to Norman Foster and Cecil Balmond. The famous diagrams comparing the Forth Bridge to animal and dinosaur skeletons (contributed by D’Arcy’s colleague in Dundee, Thomas Claxton Fidler) made many designers think about structures in a new way, and D’Arcy’s work

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[28] James D Murray, ‘How the Leopard Gets its Spots’, *Scientific American* vol 256 no 3 (1988) pp80-87. It was not until 2012 that researchers at King’s College London provided the first experimental evidence to confirm Turing and Murray’s ideas. See http://www.kcl.ac.uk/newsevents/news/newsrecords/2012/02Feb/Scientists-prove-Turings-tiger-stripe-theory-.aspx

[29] *OG&F* p1030

[30] S J Gould, ‘D’Arcy Thompson and the Science of Form’, *New Literary History* vol 2 no 2 (1971), pp229-258.

[31] Richard Dawkins, *Climbing Mount Improbable* (New York: W W Norton & Co, 1996) p200

[32] Personal communication with author, 2011

[33] Geoffrey Ozin & André Arsenault, *Nanochemistry: A Chemical Approach to Nanomaterials* (London: Royal Society of Chemistry, 2005)

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. 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 recognising the potential of D'Arcy's ideas. Henry Moore, Richard Hamilton, Jackson Pollock and Salvador Dali are among the many painters and sculptors known to have read and drawn inspiration from the book. 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 D'Arcy through Benoît Mandelbrot's work on fractals to the computer-generated imagery of Pixar and others today.[34]

Today the University of Dundee continues to promote the links between art and science, which D'Arcy demonstrated so forcefully. Although the huge Natural History Museum that he created was demolished in the 1950s, his surviving collection is now displayed in a new 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 University's Duncan of Jordanstone College of Art & Design teaches art/science modules and runs a research gallery in the School of Life Sciences called LifeSpace. Mathematical biology is now a popular MSc degree course and has become a significant area of research for the University.Through this activity and more, it is hoped that D'Arcy's work will continue to have a relevance in many fields for the foreseeable future.

www.ongrowthandform.org

[34] A notable example of this is Andy Lomas, who has created digital effects for *Avatar* and the *Matrix* films while also exhibiting his algorithm-derived art prints in galleries, citing D'Arcy as his key influence.