Abstract:

D’Arcy Thompson (1860-1948) was a grandfather of A-Life. In his book *On Growth and Form* (1917), he pioneered a type of mathematical biology which rested closely on physics, and asked many questions that are asked today by researchers in A-Life.

His theme was the nature and development of biological form, i.e. "morphology" (a word he borrowed from Goethe). He argued that biological form isn’t determined only by Darwinian evolution but also, and more fundamentally, by laws of form that apply to all species. He used geometry to display (for instance) the similarities between the skulls of various vertebrate species, or between the body-shapes of different kinds of fish.

Of Growth and Form excited many people, and was one of only six references given by Alan Turing in his 1953 paper on morphogenesis. However, it was too far before its time to be really useful. He himself recognized that he needed a more powerful mathematical language to describe series of morphological transformations. Without computers and computational concepts, D’Arcy Thompson’s ideas couldn’t be put into practice. Were he still alive today, he’d be doing A-Life.

*D'ARCY THOMPSON: A GRANDFATHER OF A-LIFE***

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I: The Grandfather of A-Life

It's well known that three core ideas of A-Life were originated many years ago, but couldn't be appreciated--still less, explored--until vastly increased computer power (and computer graphics) became available. Alan Turing's diffusion equations and John von Neumann's cellular automata were introduced with a fair degree of theoretical detail in the early-1950s. As for genetic algorithms, these were glimpsed at the same time by von Neumann, and defined by John Holland in the early-1960s. But it wasn't until the late-1980s that any of these could be fruitfully implemented.

What's not so well known is that various issues that are prominent in current A-Life were being thought about earlier still, even before the First World War. In 1917, Sir D'Arcy Wentworth Thompson (1860-1948), Professor of Zoology at the University of St. Andrews, published *On Growth and Form.* He was asking biological questions, and offering biological answers, very much in the spirit of A-Life today.

The book was immediately recognized as a masterpiece--mostly because of the hugely exciting ideas and the many fascinating examples, but also because of the superb, and highly civilized, prose in which it was written. Countless readers were bewitched by it, and begged for a second edition. That appeared during the next World War, in 1942 (six years before his death). It had grown from the initial near-800 pages to no fewer than 1116. There was plenty to chew on, there.

So why isn't it more famous now? The reason is much the same as the reason why Turing's [1952] paper on morphogenesis became widely known only fairly recently. Biologists, and especially embryologists, in the 1950s could see that Turing's work might be highly relevant, indeed fundamental, to their concerns. But, lacking both specific biochemical knowledge and computational power to handle the sums, they couldn't *do* anything with it.

The same was true of Holland's work [1962, 1975]. I remember being hugely impressed by the paper he gave at a 20-person weekend-meeting held in Devon in 1981 [Selfridge, Rissland and Arbib 1984]. Not only had he tackled evolutionary programming, but he'd solved the credit-assignment problem--a recurring, and seemingly intractable, problem in contemporary AI. I'd never heard of him, and when I got home from the Devonshire countryside I asked my AI-colleagues why they weren't shouting his name to the rooftops. Some replied that his work wasn’t usable (he’d done the mathematics, but not the programming)--and some had never heard of him either.

Similarly, D’Arcy Thompson’s war-time readers were intrigued, even persuaded, by his book. But putting it into biological practice wasn’t intellectually--or rather, technologically--possible. Today, we’re in a better position to appreciate what he was trying to do, and even to carry on where he left off.

In sum, if Turing and von Neumann (with the two Williams: Ross Ashby and Grey Walter) were the fathers of A-Life, D’Arcy Thompson was its grandfather. I don’t just mean that he could have been, if anyone had still been listening. For at least one person was listening: *On Growth and Form* was one of only six references cited by Turing at the end of his morphogenesis paper. For that reason alone, D’Arcy Thompson is worthy of respect. But in the post-WWII period, his name was still one to conjure with. I came across *On Growth and Form* as a medical student in the mid-1950s, and was entranced. Many others were too, which is presumably why an abridged (though still weighty) version was published some years later. In short, D’Arcy Thompson has inspired not only Turing, but others too.

II: Who Was D’Arcy Thompson?

D’Arcy Thompson--he’s hardly ever referred to merely as "Thompson"--was born only a year after the publication of *The Origin of Species*, and was already middle-aged when Queen Victoria died in 1901. He survived through both World Wars, dying at almost ninety years old in 1948. That was the year in which the Manchester MADM computer, for which Turing was the first programmer, became operational.

If D’Arcy Thompson had an exceptional span in life-years, he also had an extraordinary span in intellectual skills. He was a highly honoured classical scholar, who translated *Historia Animalium* for the authoritative edition of Aristotle [Thompson 1910]. In addition, he was a biologist and mathematician. Indeed, he was offered Chairs in Classics and Mathematics as well as in Zoology.

While still a teenager (if ’teenagers’ existed in Victorian England), he edited a brief book of essays from the Museum of Zoology in Dundee [Thompson 1880]. But he soon graduated to larger tomes. In his early-twenties, he prepared a near-300-page bibliography of the work on invertebrates that had been published since his birth [Thompson 1885]. At that young age, too, he edited and translated a German biologist’s scattered writings on how flowers of different types are pollinated by insects. In broom, for instance, the stamens "explode" when the bee lands on the keel of the flower, and the style curls upwards so that the stigma strikes the bee’s back. The result was a 670-page volume, for which Darwin himself wrote the Preface [Thompson 1883].

Forty years later, he was commenting on ancient Egyptian mathematics in *Nature* [Thompson 1925], and analysing thirty years’ worth of figures on the catches made by fishermen trawling off Aberdeen [Thompson 1931]. And just before the second edition of *On Growth and Form,* he put together a collection of some of his essays [Thompson 1940]. These ran from Classical biology and astronomy, through poetry and medicine, to "Games and Playthings" from Greece and

Rome; and they included popular pieces originally written for *Country Life, Strand Magazine,* and *Blackwood's Magazine* [Thompson 1940]. His last book, out a few months before he died, was a *Glossary of Greek Fishes:* a "sequel" to his volume on all the birds mentioned in ancient Greek texts [Thompson 1895, 1947]. Clearly, then, D'Arcy Thompson was a man of parts.

He was no mere list-maker, as some of the titles above might suggest. On the contrary, he was a great intellect and a superb wordsmith. His major book has been described by the biologist Peter Medawar as "beyond comparison the finest work of literature in all the annals of science that have been recorded in the English tongue" [Medawar 1958: 232]. And his intoxicating literary prose was matched by his imaginative scientific vision.

III: Biomimetics: Artefacts, But Not A-Life

For all his diverse skills, D'Arcy Thompson was no Charles Babbage. So he wasn't playing around with computers, electronic or not. Nor was he playing around with any other gizmos. In short, he wasn't doing biomimetics.

Biomimetics involves making material analogues of the physical stuff of living things, in order to investigate its physico-chemical properties. Vaulted roofs modelled on leaf-structure count, since they are testing/exemplifying the tensile properties of such physical structures. But automata don't. Even if the movements of specific bodily organs are being modelled--as in Jacques de Vaucanson's [1738-1742] flute-player, which moved its tongue, lips, and fingers [1738/1742]--the physical *stuff* is not.

Perhaps the first example of biomimetics, and certainly one of the most startling, was due to Henry Cavendish. In 1776, Cavendish nominated Captain Cook for election to the Royal Society. Having just completed his second great voyage of discovery, Cook had exciting tales to tell of exotic fish and alien seas. But so did Cavendish. For, in the very same year, he'd built an artificial electric fish and lain it in an artificial sea [Wu 1984; Hackman 1989].

Its body was made of wood and sheepskin, and its electric organ was two pewter discs, connected by a brass chain to a large Leyden battery; its habitat was a trough of salt water. Cavendish's aim was to prove that "animal electricity" is the same as the physicist's electricity, not an essentially different (vital) phenomenon. His immobile 'fish' wouldn't have fooled anyone into thinking it was a real fish, despite its fish-shaped leather 'body'. But--and this was the point--it did deliver a real electric shock, indistinguishable from that sent out by a real torpedo fish.

Cavendish had intended his artificial fish to deliver an intellectual shock, as well as a real one. His aim was to demystify a vital phenomenon, to show the continuity between the physical and the organic--and, of course, to display the physical principle underlying the living behaviour.

He thought this shocking hypothesis to be so important that he invited some colleagues into his laboratory to observe the experiment--so far as we know, the only occasion on which he did so [Wu 1984: 602]. Certainly, such an invitation from the taciturn Cavendish was a remarkable event: an acquaintance said that he "probably uttered fewer words in the course of his life than any man who ever lived to fourscore years, not at all excepting the monks of la Trappe" [Lord Brougham, quoted in n.a. 1990: 975].

(Oliver Sacks [2001] has suggested that Cavendish’s unsociability was due to Asperger’s syndrome. If so, he was--perhaps--in good company: the same posthumous ’diagnosis’ has been made of Einstein and Newton [Baron-Cohen & James 2003].)

But if Cavendish’s doubly shocking demonstration was an exercise in biology, and simultaneously in physics, it wasn’t an exercise in mathematics. That’s to say, it wasn’t an early example of A-Life.

A-Life is abstract in nature. On the one hand, it’s concerned with "life as it could be," not only "life as it is" [Langton 1989]. On the other hand, it studies life-as-it-is not by putting it under the microscope, or twirling it around in a test-tube, but by seeking its logical-computational principles. Even A-Life work on biochemistry is looking for abstract principles, not--or not only--for specific molecules [e.g. Drexler 1989; Szostak, Bartel, & Luisi 2001; Kauffman 2003].

Cavendish’s experiment couldn’t have been done without the artificial fish in its bath of conducting fluid, because his aim was to reproduce the same physical phemomenon (electrical conductivity) that occurs in some living things. Biomimetics requires physical mimesis. But A-Life doesn’t.

Someone might even say that A-Life doesn’t need *any* artefacts: not fish-in-fluid, nor computers either. If artefacts are needed at all, then just three will suffice: pencil, paper, and armchair. In principle, that’s so. We saw in Section I that some hugely important A-Life work was done either without the aid of computers or (in Turing’s case) with the aid only of very primitive machines. In practice, however, computers are almost always needed.

It’s possible, in other words, for someone to do mathematical biology without being able to do computational biology. They may be able to define the mathematical principles, and even to intuit their general implications, without being able to calculate their consequences in any detail. That’s precisely the position which D’Arcy Thompson was in. After all, computers weren’t a feature of the Edwardian age.

IV: First Steps in Mathematical Biology

Isolated examples of mathematically expressed biological research were scattered in the pre-twentieth century literature. But mathematical biology as an all-encompassing and systematic approach was attempted only after the turn of the century--by D’Arcy Thompson.

Although Darwin had written the Preface for his first ’real’ book, D’Arcy Thompson had become increasingly critical of Darwinian theory. An early intimation of this was in his paper "Some Difficulties of Darwinism," given in 1894 to an Oxford meeting of the British Association for the Advancement of Science (one of Babbage’s many brainchildren, as of 1831). His book, over twenty years later, explained at length why he felt Darwinism to be inadequate as an explanation of the living creatures we see around us.

Like some maverick modern biologists [Webster & Goodwin 1996; Goodwin 1994; Kauffman 1993], he regarded natural selection as strictly secondary to the origin of biological form. The origin of form, he said, must be explained in a different way.

He integrated a host of individual biological facts within a systematic vision of the order implicit in living organisms. That is, he used various ideas from mathematics not only to describe, but also to explain, fundamental features of biological form. He wasn't content, for example, to note that patterns of leaf-sprouting on plants may often be described by a Fibonacci number-series (such as 0,1,1,2,3,5,8,13,21...). He converted this finding from a mathematical curiosity into a biologically intelligible fact, by pointing out that this is the most efficient way of using the space available.

Significantly, he often combined 'pure' mathematical analysis with the equations of theoretical physics. In this way, he tried to explain not only specific anatomical facts (such as the width and branching-patterns of arteries, relative to the amount of blood to be transported), but also why certain forms appear repeatedly in the living world.

D'Arcy Thompson referred to countless examples of actual organisms, but he had in mind also *all possible* life-forms. As he put it:

"[I] have tried in comparatively simple cases to use mathematical methods and mathematical terminology to describe and define the forms of organisms.... [My] study of organic form, which [I] call by Goethe's name of Morphology, is but a portion of that wider Science of Form which deals with the forms assumed by matter under all aspects and conditions, and, in a still wider sense, with *forms which are theoretically imaginable"* [1942: 1026; italics added].

For D'Arcy Thompson, then, the shapes of animals and plants aren't purely random: we can't say "Anything goes." To the contrary, developmental and evolutionary changes in morphology are constrained by underlying general principles of physical and mathematical order.

V: Goethe's Morphology

As his own acknowledgment (above) made clear, D'Arcy Thompson's work was closely related to Johann von Goethe's (1749-1832) rational morphology. Goethe had coined the word "morphology," meaning the study of organized things. It concerns not just their external shape, but also their internal structure and development--and, crucially, *their structural relations to each other.* Goethe had intended morphology to cover both living and inorganic nature, even including crystals, landscape, language, and art. But D'Arcy Thompson's interest was with its application to biology.

In his *Essay on the Metamorphosis of Plants*, Goethe [1790] had argued that superficially different parts of a flowering plant--such as sepals, petals, and stamens--are derived by transformations from the basic, or archetypal, form: the leaf. Later, he posited an equivalence (homology) between the arms, front-legs, wings, and fins of different animals. All these, he said, are different transformations of the fore-limb of the basic vertebrate type. And all bones, he claimed, are transformations of vertebrae. In other words, he combined meticulous naturalistic observation with a commitment to the fundamental unity of nature.

For instance, he’s widely credited with a significant discovery in comparative anatomy. Namely, that the intermaxillary bone--which bears the incisors in a rabbit’s jaw--exists (in a reduced form) in the human skeleton, as it does in other vertebrates. (Strictly, he *rediscovered* this fact [Sherrington 1942: 21f.], and *restated* the claim that sepals are a type of leaf [Goethe 1790: 73].) The issue was "significant" because some people had used the bone’s seeming absence to argue that God created a special design for human beings, marking them off from the animals. Goethe, by contrast, related human skulls to the archetypal vertebrate skull, much as he related sepals to the archetypal leaf.

Goethe didn’t think of morphological transformations as temporal changes, still less as changes due to Darwinian evolution--which was yet to be defined. Rather, he saw them as abstract, quasi-mathematical, derivations from some neo-Platonic ideal in the mind of God. But these abstractions could be temporally instantiated.

So in discussing the development of plants, for instance, he referred to actual changes happening in time as the plant grows. He suggested that sepals or petals would develop under the influence of different kinds of sap, and that external circumstances could lead to distinct shapes, as of leaves developing in water or in air--a suggestion that D’Arcy Thompson took very seriously, as we’ll see.

The point of interest here is that Goethe had focussed attention on the restricted range of basic forms ("primal phenomena") in the organic world. He encouraged systematic comparison of them, and of the transformations they could support. He also suggested that only certain forms are possible: we can imagine other living things, but not just *any* life-forms. In a letter of 1787, he wrote:

"With such a model [of the archetypal plant *(Urfplanz)* and its transformations] ... one will be able to contrive an infinite variety of plants. They will be *strictly logical* plants--in other words, *even though they may not actually exist, they could exist.* They will not be mere picturesque and imaginative projects. They will be imbued with inner truth and necessity. And the same will be applicable to all that lives" [quoted in Nisbet 1972: 45; italics added].

Similarly, in his essay on plant metamorphosis [1790], he said: "Hypothesis: All is leaf. This simplicity makes possible the greatest diversity".

Critics soon pointed out that he overdid the simplicity. He ignored the roots of plants, for instance. His excuse was telling:

"It [the root] did not really concern me, for what have I to do with a formation which, while it can certainly take on such shapes as fibres, strands, bulbs and tubers, remains confined within these limits to a dull variation, in which endless varieties come to light, but without any intensification [of archetypal form]; and it is this alone which, in the course marked out for me by my vocation, could attract me, hold my attention, and carry me forward" [quoted in Nisbet 1972: 65].

To ignore apparent falsifications of one’s hypothesis so shamelessly seems utterly unscientific in our Popperian age. And some of Goethe’s contemporaries complained about it, too. But his attitude stemmed from his idealist belief in the essential unity of science and aesthetics. He even compared the plant to a superb piece of architecture, whose foundations--the roots--are of no interest to the viewer. More generally: "Beauty is the manifestation of secret laws of nature which, were it not for their being revealed through beauty, would have remained unknown for ever" [quoted in Nisbet 1972: 35]. For Goethe, and perhaps for D’Arcy Thompson too, this language had an import much richer than the familiar appeals to theoretical ’simplicity,’ ’symmetry,’ or ’elegance.’

Questions about such abstract matters as the archetypal plant were very unlike those being asked by most physiologists at the time. If a body is not just a flesh-and-blood mechanism, but a transformation of an ideal type, how it happens to work--its mechanism of cords and pulleys--is of less interest than its homology.

Indeed, for the holist Goethe the mechanism may even depend on the homology. Perhaps it’s true that a certain kind of sap, a certain chemical mechanism, will induce a primordial plant-part to develop into a sepal rather than a petal. But what’s more interesting--on this view--is that sepals and petals are the structural possibilities on offer. How one describes the plant or body part in the first place will be affected by the type, and the transformations, supposedly expressed by it.

It’s not surprising, then, that Goethe was out of sympathy with the analytic, decompositional methods of empiricist experimentalism. By the same token, anyone following in his footsteps--as D’Arcy Thompson did--would be swimming against that scientific tide.

Initially, Goethe’s morphology attracted scepticism even from descriptive (non-experimental) biologists. But shortly before his death, his ideas were publicly applauded by Etienne Geoffroy Saint-Hilaire [Merz 1904, ii: 244]. Geoffroy agreed with him that comparative anatomy should be an exercise in "rational morphology," a study of the successive transformations--rational, not temporal--of basic body-plans.

After his death, Goethe’s work was cited approvingly even by Thomas Huxley and the self-proclaimed mechanist Helmholtz. Indeed, Helmholtz credited Goethe with "the guiding ideas [of] the sciences of botany and anatomy ... by which their present form is determined," and praised his work on homology and transformation as "ideas of infinite fruitfulness" [Helmholtz 1853: 34, 30].

"Infinite fruitfulness" isn’t on offer every day. So why were Goethe’s ideas largely forgotten by the scientific community? Surely, such an encomium from such a high-profile scientist--and committed mechanist--as Helmholtz would be enough to guarantee close, and prolonged, attention?

Normally, yes. However, only six years after Helmholtz spoke of Goethe’s "immortal renown" in biology, Darwin (1809-1882) published *On the Origin of Species by Means of Natural Selection* [1859]. This radically changed the sorts of enquiry that biologists found relevant. One might even say that they changed the sorts of enquiry that biologists found *intelligible* [cf.

Jardine 1991]. Biological questions were now posed in ways that sought answers in terms of either mechanistic physiology or Darwinian evolution.

Soon, genetics became an additional source of enquiry. The neo-Darwinian mix of physiology, evolution, and genetics was a heady brew. It quickly became the biological orthodoxy, eclipsing *Naturphilosophie* in all its forms. Darwin, like Goethe, encouraged systematic comparisons between different organs and organisms. But he posited no ideal types. He explained morphological similarity in terms of contingency-ridden variation and selective descent, or coincidental likeness between environmental constraints. In short, morphological self-organization largely *disappeared* as a scientific problem, surviving only in embryology.

Charles Sherrington even said that "were it not for Goethe’s poetry, surely it is true to say we should not trouble about his science," and that metamorphosis is "no part of botany today" (Sherrington 1942: 23, 21).

VI: From Morphology to Mathematics

Ironically, Sherrington’s remark was published in the very same year as the long-awaited new edition of *On Growth and Form.* Although Goethe himself is now largely ignored by biologists (but see [Webster and Goodwin 1991: esp. chaps. 1 & 5]), his questions have survived--thanks, largely, to D’Arcy Thompson.

Like Goethe, whom he quoted with approval several times in his book, D’Arcy Thompson sought an abstract description of the anatomical structures and transformations found in living things--indeed, in all possible things. So he discussed the reasons for the spherical shape of soap-bubbles, for instance. His reference (above) to "forms which are theoretically imaginable" recalls Goethe’s reference to "strictly logical plants"--in other words, "life as it could be." And like Goethe, he believed that certain forms were more natural, more likely, than others. In some sense, he thought, there are "primal phenomena."

Also like Goethe--though here, the analogy becomes more strained--he asked questions about the physical mechanisms involved in bodily growth. But his philosophical motivation for those questions was importantly different. Although D’Arcy Thompson was sympathetic to some of the claims of the *Naturphilosophen,* he wasn’t a fully paid-up member of their club. Indeed, he opened his book by criticizing Kant and Goethe, complaining that they had ruled mathematics out of natural history [Thompson 1942: 2].

In part, he was here expressing his conviction that "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" [p. 1096f.]. This conviction wasn’t shared by his professional colleagues: "Even now, the zoologist has scarce begun to dream of defining in mathematical language even the simplest organic forms" [p. 2]. But in part, he was saying that physics--real physics--is crucially relevant for understanding "Form."

The idealist Goethe had seen different kinds of sap as effecting the growth of sepal or petal, but for him those abstract possibilities had been generated by the divine intelligence selfcreatively immanent in Nature. D'Arcy Thompson, by contrast, argued that it is real physical processes, instantiating strictly physical laws, which generate the range of morphological possibilities. Certainly, those laws conform to abstract mathematical relationships--to projective geometry, for example. But biological forms are made possible by underlying material-energetic relations.

Accordingly, D'Arcy Thompson tried to relate morphology to physics, and to the dynamical processes involved in bodily growth. He suggested that very general physical (as opposed to specific chemical or genetic) constraints could interact to make some biological forms possible, or even necessary, while others are impossible.

Had he lived today, D'Arcy Thompson would doubtless have relished the work of Ralph Linsker [1986, 1988, 1990] and Christoph von der Malsburg [1973, 1979] on the self-organization of feature-detectors in sensory cortex. For this explains why we should expect to find systematic neuroanatomical structure in the brain, as opposed to a random ragbag of individually effective detector-cells. Moreover, the "why" isn't a matter of selection pressures, but of spontaneous self-organization. But this recent research required computational concepts and computing power (not to mention anatomical data) that he simply didn't have. He could use only the mathematics and physics available in the early years of the century.

Although D'Arcy Thompson wasn't the first biologist to study bodies, he might be described as the first biologist who took *embodiment* seriously. The physical phenomena he discussed included diffusion, surface forces, elasticity, hydrodynamics, gravity, and many others. And he related these to specific aspects of bodily form.

His chapter "On Magnitude," for example, argued both that size can be limited by physical forces and that the size of the organism determines which forces will be the most important. Gravity is crucial for mice, men, and mammoths, but the form and behaviour of a water-beetle may be conditioned more by surface-tension than by gravity. A bacillus can in effect ignore both, being subject rather to Brownian motion and fluid viscosity. Similarly, the fixed ratio between volume and surface-area is reflected, in a single cell or a multicellular animal, in respiratory surfaces such as the cell-membrane, feathery gills, or alveolar lungs. Again, his fascinating discussion of "The Forms of Cells" suggested, among many other things, that the shape and function of cilia follow naturally from the physics of their molecular constitution.

Perhaps the best-known chapter of *On Growth and Form*, and the one which had the clearest direct influence, was entitled "On the Theory of Transformations, or the Comparison of Related Forms." This employed a set of two-dimensional Cartesian grids to show how differently shaped skulls, limb-bones, leaves, and body-forms are mathematically related. One form could generate many others, by enlargement, skewing, and rotation.

So, instead of a host of detailed comparisons of individual body-parts bearing no theoretical relation with each other, anatomists were now being offered descriptions having some analytical unity.

To be sure, these purely topological transformations couldn't answer questions about more radical alterations in form. The gastrulation of an embryo, for example, couldn't be explained in this way (see [Turing 1952]). And only very few zoologists--of whom Medawar was one--tried to use D'Arcy Thompson's specific method of analysis. But his discussion inspired modern-day allometrics: the study of the ratios of growth-rates of different structures, in embryology and taxonomy.

VII: More Admiration than Influence

One didn't need to be doing allometrics to admire D'Arcy Thompson. By mid-century, he was widely revered as a scientist of exceptional vision [Hutchinson 1948; Le Gros Clark & Medawar 1945]. The second edition of *On Growth and Form* was received with excitement in 1942, the first (of only 500 copies) having sold out twenty years before. Reprints had been forbidden by D'Arcy Thompson himself, while he worked on the revisions, and second-hand copies had been fetching ten times their original price.

However, only a decade after the second edition, which people had awaited so eagerly for years, the advent of molecular biology turned him virtually overnight into a minority taste. As we've seen, much the same had happened to his muse Goethe, whose still-unanswered biological questions simply stopped being asked when Darwin's theory of evolution came off the press in 1859. By the end of the 1960s, only a few biologists regarded D'Arcy Thompson as more than a historical curiosity.

One of these was Conrad Waddington (1905-1975), a developmental biologist at the University of Edinburgh (whose theory of "epigenesis" influenced Jean Piaget [Boden 1994: introd., 98-101]). Waddington continually questioned the reductionist assumption that molecular biology can--or rather, will--explain the many-levelled self-organization of living creatures. It's hardly surprising, then, that D'Arcy Thompson was often mentioned in his 'invitation only' seminars on theoretical biology, held in the late 1960s at the Rockefeller Foundation's Villa Serbelloni on Lake Como [Waddington 1966-1972].

But Waddington, too, was a maverick, more admired than believed. His theory of epigenesis couldn't be backed up by convincing empirical evidence, whether in the developing brain or in the embryo as a whole. Only after his death did his ideas gain ground. Significantly, the proceedings of the first A-Life conference were dedicated to him [Langton 1989: xiii].

D'Arcy Thompson's most devoted admirers, however, had to concede that it was difficult to turn his vision into robust theoretical reality. Despite his seeding of allometrics, his direct influence on biology was less strong than one might expect, given the excitement (still) experienced on reading his book.

Even the subsequent attempts to outline a mathematical biology eschewed his methods. Joseph Woodger's [1929, 1937] axiomatic biology, for instance, owed more to mathematical logic and the positivists' goal of unifying science [Neurath 1939] than to D'Arcy Thompson. And Turing's mathematical morphology employed numerically precise differential equations, not geometrical transformations. In short, D'Arcy Thompson figured more as inspirational muse than as purveyor of specific biological theory or fact.

The reason why his influence on other biologists, although "very great"," was only "intangible and indirect" [Medawar 1958: 232] is implied by his own summary comment.

At the close of his final chapter, he recalled the intriguing work of a naval engineer who, in 1888, had described the contours and proportions of fish "from the shipbuilder's point of view." He suggested that hydrodynamics must limit the form and structure of swimming creatures. But he admitted that he could give no more than a hint of what this means, in practice. In general, he said:

"Our simple, or simplified, illustrations carry us but a little way, and only half prepare us for much harder things.... *If the difficulties of description and representation could be overcome*, it is by means of such co-ordinates in space that we should at last obtain an adequate and satisfying picture of the processes of deformation and the directions of growth" [1942: 1090; italics added].

VIII: Echoes in A-Life

This early exercise in mathematical biology resembled current work in A-Life in various ways. So much so, that one would expect D'Arcy Thompson, were he to return today, to recognize the theoretical point of most work in A-Life, even though he'd be bemused by its high-tech methodology.

For instance, he'd be fascinated by Dimitri Terzopoulos' lifelike computer-animation of fish, with its detailed interplay of hydrodynamics and bodily form [Terzopoulos et al. 1994]. These 'fish' weren't robots, but software-creatures existing in a computer-generated virtual world. Whereas Cavendish's 'fish' was a solitary object lying inert in a dish of water, these were constantly in motion, sometimes forming hunter-hunted pairs or co-moving schools. Each one was an autonomous system, with simple perceptual abilities that enabled it to respond to the world and to its fellows. The major bodily movements, with their associated changes in body-shape, resulted from twelve internal muscles (conceptualized as springs). The computerized fish learned to control these in order to ride the (simulated) hydrodynamics of the surrounding sea-water. A host of minor movements arose from the definitions of seventy-nine other springs and twenty-three nodal point masses, whose (virtual) physics resulted in subtly lifelike locomotion.

He'd be intrigued, also, by Karl Sims' [1994] A-Life evolution of decidedly *un-lifelike* behaviour, as a result of a specific mistake in the simulated physics. He'd be the first to realize that in a physical world such as that defined (mistakenly) by Sims, these strange 'animals' would be better adapted to their environment than those which actually exist. For sure, he'd be interested in programmes of research that systematically varied physical parameters to see what sorts of creatures would result. And he'd be fascinated by Randall Beer's studies of locomotion in cockroach-robots [Beer 1990, 1995; Beer & Gallagher 1992]. For, unlike Terzopoulos and Sims, Beer subjected his computer-creatures to the unforgiving discipline of the real physical world.

He'd applaud Greg Turk's [1991] models of diffusion gradients, delighting in Turk's demonstration of how to generate leopard-spots, cheetah-spots, lion-fish stripes, and giraffe-reticulations. And he'd doubtless be pleased to learn that Turk's equations were based on

Turing's, which in turn were inspired by D'Arcy Thompson himself (see above).

He'd sympathize with biologists such as Brian Goodwin and Stuart Kauffman, who see evolution as grounded in general principles of physical order [Webster & Goodwin 1996; Goodwin 1994; Kauffman 1993]. He'd agree with A-Lifers who stress the dynamical dialectic between environmental forces and bodily form and behaviour. He might well have embarked on a *virtual* biomimetics: a systematic exploration of the effects of (simulated) physical principles on (simulated) anatomies. And he'd certainly share A-Life's concern with *life as it could be* --his "theoretically imaginable forms"--rather than life as we know it.

IX: Difficulties of Description

The "difficulties of description and representation" bemoaned by D'Arcy Thompson remained insuperable for more than half a century after publication of those first 500 copies of his book. Glimpses of how they might be overcome arose (in the early-1950s) a few years after his death. Actually overcoming them took even longer. Or perhaps one should rather say it *is taking* even longer, for we haven't answered all of his questions yet.

Despite the deep similarity in spirit between D'Arcy Thompson's work and A-Life research, there are three important, and closely related, differences. Each of these reflects his historical situation--specifically, the fact that his work was done before the invention of computers.

One difference concerns the practical usefulness of computer technology, and shows why (contrary to the suggestion noted above) A-Life's artefacts are not, in fact, dispensable. The other two concern limitations on the mathematical concepts available when D'Arcy Thompson was writing: in his words, the difficulties of description and representation that needed to be overcome.

First, D'Arcy Thompson was able to consider only broad outlines, largely because he had to calculate the implications of his theories using hand and brain alone. Today, theories with richly detailed implications can be stated and tested with the help of superhuman computational power. The relevant theories concern (for instance) the hydrodynamics of fish; the interactions between various combinations of diffusion gradients; and processes of evolution and co-evolution, occurring over many thousands of generations.

In addition, we can now study chaotic phenomena (which include many aspects of living organisms), where tiny alterations to the initial conditions of a fully deterministic system may have results utterly different from those in the non-altered case. These results can't be predicted by approximation, or by mathematical analysis. The only way to find out what they are is to watch the system--or some computer specification of it--run, and see what happens. In all these cases, the 'help' A-Life gets from computers isn't an optional extra, but a practical necessity.

Second, D'Arcy Thompson's theory, though relatively wide in scope, didn't encompass the most general feature of life: self-organization as such. Instead, it considered many specific examples of self-organization. This isn't surprising. Prior to computer science and information theory, no precise language was available in which this could be discussed.

And third, although he did consider deformations produced by physical forces, D'Arcy Thompson focussed more on structure than on process. This is characteristic of pre-computational theories in general. In anthropology, for example, Claude Levi-Strauss in the early-1950s posited cognitive *structures* (based on binary opposition) to explain cultural phenomena, leaving his successors--notably Daniel Sperber--to consider the *processes* involved in communication and cultural evolution (see Boden 2006: chap. 8.vi). Prior to computer science, with its emphasis on the exact results of precisely specified procedures, scientists lacked ways of expressing--still less, of accurately modelling (and tracking)--the details of change.

Uniform physical changes could be described by linear differential equations, to be sure. And Babbage [1838] could even lay down rules, or programs (for his Difference Engine), determining indefinitely many "miraculous" discontinuities. But much as Babbage (as he admitted) couldn't program the transformation of caterpillar into butterfly, so D'Arcy Thompson's mathematics couldn't describe the morphological changes and dynamical bifurcations that occur in biological development.

X: And What Came Next?

One might have expected that cybernetics would provide some of the necessary advances in descriptive ability. The scope of cyberneticians' interests, especially on D'Arcy Thompson's home ground, the UK, was very wide [Boden 2006: chap. 4]. Among other things, it included various exercises in mathematical biology; and it used robots and (analogue) computer modelling as a research technique. The study of "circular causal systems" drew on mainstream ideas about metabolism and reflexology, not on the morphological questions that interested D'Arcy Thompson. But the cybernetic movement considered some central biological concerns now at the core of A-Life: adaptive self-organization, the close coupling of action and perception, and the autonomy of embodied agents.

It even made some progress. For instance, Ashby's [1952] "design for a brain," and his Homeostat machine, depicted brain and body as dynamical physical systems. And Grey Walter's [1950] tortoises, explicitly intended as "an imitation of life," showed that lifelike behavioural control can be generated by a very simple system.

However, the cybernetics of the 1950s was hampered both by lack of computational power and by the diversionary rise of symbolic AI. Only much later--and partly because of lessons learned by symbolic AI--could cybernetic ideas be implemented more convincingly. (Even so, recent dynamical approaches suffer a limitation shared by cybernetics: unlike classical AI, they can't easily represent hierarchical structure, or detailed structural change.)

As it turned out, it was physics and computer science--not cybernetics--which, very soon after D'Arcy Thompson's death in 1948, produced mathematical concepts describing the generation of biological form. Indeed, two of the founding-fathers of computer science and AI, Turing and von Neumann, were also the two founding fathers of A-Life. (Von Neumann's intellectual range was even greater than Turing's, including chemical engineering for example [Ulam 1958].)

Around mid-century, they each developed accounts of self-organization, showing how simple processes could generate complex systems involving emergent order. They might have done this during D'Arcy Thompson's lifetime, had they not been preoccupied with defence-research. While Turing was code-breaking at Bletchley Park, von Neumann was in Los Alamos, cooperating in the Manhattan Project to design the atom bomb.

The end of the war freed some of their time for more speculative activities. Both turned to abstract studies of self-organization. Their new theoretical ideas eventually led to a wide-ranging mathematical biology, which could benefit from the increasingly powerful technology that their earlier work had made possible.

In sum, D'Arcy Thompson didn't get there first. He didn't really get there at all. But he did pave the way.

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