IN THE BEAT OF A HEART
LIFE, ENERGY, AND THE UNITY OF NATURE

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"I HAVE TAKEN TO MATHEMATICS"

As he entered his forties, in the first decade of the twentieth century, D'Arcy Wentworth Thompson looked back on his life with some bitterness. He was stagnating, teaching zoology at a provincial university in a coarse, industrial Scottish city. His fellow scientists, when they thought of him at all, seemed to view him as a dilettante and showed no interest either in his ideas or in giving him a better job. He, in turn, did not think much of their politicking and lazy orthodoxy—"the brethren," he called them. In his bottom drawer was a translation of Aristotle's work on animals, still unfinished 30 years after it was begun.

Fortunately, Thompson had something to take his mind off his frustrations. For the past 20 years, besides doing the everyday, unspectacular work of the Edwardian biology professor—describing, counting, and cataloguing living specimens—he had quietly been building a new foundation for his science from the techniques and concepts of physics and mathematics. These other fields, he believed, could describe and explain how living things were constructed and how they functioned.

This was radical work. Many scientists of the time believed that living things were fundamentally different from any chemical or
physical system and beyond the powers of physics or chemistry to explain. This school of thought held that living matter was imbued with unique properties or animated by a special force—a philosophy called vitalism. To vitalists, biology's task was to seek out the differences between living and dead things, not the commonalities. Such a view was not merely the territorial behavior or professional blinkeredness of biologists. Even eminent physicists such as James Clerk Maxwell, whose work revolutionized our understanding of electromagnetism and gases, believed that the chemistry of atoms, molecules, and elements could not explain living matter and that the laws of thermodynamics could not explain how bodies worked. And few biologists knew any mathematics, partly because it seemed irrelevant to their discipline and partly because of a feeling that to explain living forms in this way, to show that they fell within the orbit of sciences developed to explain dead matter, belittled them in a way that was almost immoral.

But Thompson was different. His familiarity with, and love of, the works of Aristotle, Pythagoras, and Plato had given him an expertise in mathematics, particularly geometry, far beyond that of most zoologists. He was a voracious polymath, willing to take inspiration anywhere. Classical, or renaissance, or enlightenment thinking was not obsolete; it was fundamental: "A fact discovered yesterday is balanced by the history of two thousand years," he wrote. His intellectual roots lay in the time when educated people read and pondered everything, seeing no distinction between different branches of scholarship. And instead of seeing it as a debasement to bring mathematics into biology, he had the Greek belief in that discipline's beauty and perfection.

Another thing that made Thompson an unusual biologist is that he thought his science should, following the example of physics, look for big answers and grand, overarching theories. Faced with the dazzling complexity of life, biology has traditionally been a science built of details and descriptions—from Linnaeus's classification of species to the modern drive to sequence genomes. But Thompson belonged to another strand, which asks: Is there an underlying unity to nature? Can we discern patterns running through life's diversity? Are there rules that might explain these patterns? And if so, are these rules the product of chance and history, or can we perceive them as the inevitable product of constant forces and conditions? And can these forces and conditions be expressed in the language of mathematics, physics, and chemistry?

In 1917, Thompson published his thoughts on these matters in a book, *On Growth and Form*. The work brought him intellectual fulfillment and professional recognition, and it has become a scientific and literary classic, second only to Darwin's works in the pantheon of biological writings. But it was a beginning, not an end—"all preface," said Thompson. We have yet to reach the end: In the intervening century, his preoccupations have never occupied center stage in biology, but neither have they gone away. His questions still need answers.

This is the story—with some detours—of D'Arcy Thompson's strand of biology and of a century-long attempt to build a unified theory, based on the laws of physics and mathematics, of how living things work. At the story's heart is the study of something that Thompson called "a great theme"—the role of energy in life. "Morphology," he wrote, "is not only a study of material things and of the forms of material things, but it has its dynamical aspect, under which we deal with the interpretation... of the operations of Energy." Energy is life, and life's currency. It unites and divides all living things; its flow from one place to another controls everything from cells to forests. If you follow it, you can understand how nature works. As the physicist Ludwig Boltzmann wrote in 1886: "Available energy is the main object at stake in the struggle for existence and the evolution of the world."

The way that energy affects life depends on the size of living things. Size is the most important single notion in our attempt to understand energy's role in nature. Here, again, we shall be following Thompson's example. After its introduction, *On Growth and Form* ushers the reader into a physical view of living things with a chapter titled "On Magnitude," which looks at the effects of body size on biology, a field called biological scaling. Growth and form, Thompson explains, are both questions of body size. The former represents changes in size with time, and "the form of an object is defined when we know its magnitude."

We are going to see how far an understanding of biological energy, viewed through the lens of body size, will get us in understanding life, from how much food we need, to how long we live and how many
offspring we can be expected to produce, to the way that species are spread across the globe and how tropical forests get to be so exciting. D’Arcy Thompson will point the way, as both figurehead and navigator.

Father and Son

D’Arcy Wentworth Thompson took his name from his father. His father took his name from Captain D’Arcy Wentworth of the British army who, in April 1829, traveled on the sailing barque Georgiana from the Australian penal colony of Van Diemen’s Land to Sydney. A lack of other work had driven the ship’s master, John Skelton Thompson, to take a job transporting British convicts to Australia. The Georgiana’s journey to the southern hemisphere had been hard, beset by storms, sickness, and death among the prisoners and knife fights among the crew. Thompson had an additional worry: His new and pregnant bride, Mary, was aboard—the ship was their only home. She gave birth to a son on April 17, with the ship in sight of its destination, where it would soon unload its troublesome cargo.

As a young man of good character, Captain Wentworth offered himself as the child’s godfather, and so also gave D’Arcy Wentworth Thompson his name. Mother and son arrived back in Europe two years later, settling in Brussels. John Thompson did not, having died of sunstroke in the West Indies. The family was not well off, but the boy won a scholarship to Christ’s Hospital School in England, where he spent what he called a “dreary, weary boyhood,” not seeing his mother for 12 years. At school Thompson excelled in the classics. On holidays he walked the countryside alone and learned to imitate bird calls. At the age of 19, he won another scholarship, allowing him to continue his classical studies at Trinity College in Cambridge. After graduating, he applied for a fellowship at Trinity but was turned down, reputedly because he had once attended the college’s chapel in his dressing gown. Instead, he got a job as a classics master at the Edinburgh Academy, where his pupils included Robert Louis Stevenson, and his imaginative teaching, rejection of corporal punishment, and advocacy of higher education for women won him renown and opprobrium in roughly equal quantities.

In 1858, Thompson met and fell in love with Fanny Gamgee. The Gamgees were a prominent Edinburgh scientific family, and Fanny’s father Joseph and her brother John both held lectureships in veterinary medicine. Like the Thompsons, the Gamgees were self-made and well traveled. Joseph, an influential horse doctor, had learned his skills in Europe, where he served an Italian prince before returning to study in London; to save money for his fees, he made the journey on foot. D’Arcy and Fanny were married in 1859, and Fanny gave birth to a son on May 2 of the following year. A week later she died of puerperal fever, at age 21.

The loss of his wife was a hammer blow to the husband’s mind and health. He was unable to care for his newborn son, and so the baby was sent to Fanny’s parents, to be raised by a maiden aunt, Clementina. Fanny’s mother named the boy after his father. Thompson senior recovered and emigrated to Galway, Ireland, in 1863, where he settled, began teaching again, and eventually remarried. He left his son behind, although the two developed a deep bond, writing often and visiting occasionally. Thompson junior inherited his father’s interests in the classics and natural history, spending his weekends identifying the local plants and fossils, and fishing in rock pools. The Edinburgh Academy—the son following as a pupil where his father had taught—took care of the book learning, covering the classics, the Bible, mathematics, and languages. In 1877, Thompson was top in his class in the final exam. He made up for the curriculum’s lack of science by compiling a list of all the species of plants and animals he could find on the school grounds. He inherited his physique from the Thompson family’s Scandinavian ancestors, growing to over 6 feet tall, with red-blond hair and piercing blue eyes.

In 1878, the younger D’Arcy Wentworth Thompson went to Edinburgh University with the intention of studying medicine. As his education progressed, however, he became more interested in zoology, botany, paleontology, and the debates around evolution that were wracking the university. He published his first scientific paper, on a fossil seal, during this time. But the notion that biology was a discipline in its own right was new and studying it involved switching universities, to Cambridge, which had appointed its first professor in
the subject in 1866. Grandfather Joseph warned him not to be seduced by specialization: “The new fangled idea of subjects being so great that only parts must be undertaken by one man is a consummate absurdity.” Thompson got the money to attend Cambridge by winning a scholarship, but it wasn’t enough to live on, so he taught Greek and wrote for encyclopedias. Some of this work brought academic as well as financial benefit: One of his first significant scientific endeavors was to translate a German book on pollination. Charles Darwin—who had also studied medicine at Edinburgh before moving to Cambridge—wrote an admiring preface, but died before the book was published in 1883. Thompson had visited Germany in the summer of 1879 to learn the language—an essential skill for any zoologist, as the country was the center of biological science.

The biographies of Victorian scholars often make it seem as if people had more time, or energy, or talent back then. Besides making money and pursuing his studies, it was in Cambridge that Thompson embarked on the translation, in collaboration with his father, of Aristotle’s Historium Animalium. He was also active in university life, becoming a leading light of the university’s debating society. Despite all this, he seems never to have fit in, either at school or university. A contemporary at the former remembered him as “a queer fellow—there was always something about him we couldn’t understand,” and a professor at Cambridge once told him, “You know you haven’t got many friends.” Thompson was shocked, but on reflection saw the truth in this, and the feeling of friendlessness, of being apart from other people, remained with him throughout his life. But he also wore his loneliness as a badge of intellectual integrity, a pride enhanced by a belief that he had inherited the trait from his father. “He never hunted with the pack, nor barked, growled, yelped with them either,” he wrote. “And, thank God, no more do I!”

Thompson also inherited his father’s attitude toward work. Thompson senior believed it was impossible to reconcile ambition with integrity and that pushing oneself forward was, “[something] that a gentleman, a pukka Sahib, does not do.” Likewise, his son disdained the maneuvering that an academic career demands—being nice to the right people, publishing regularly on the right subjects—and often pro-

claimed his contempt for careerism. And while he could be charming, devoted, and loyal, he could also be inscrutable, volatile, impulsive, and brusque, particularly to fellow scientists. Such aloofness hardly enhanced his employability. The Cambridge higher-ups thought he spread himself too thinly, starting more projects than he finished and never knocking down to the one solid piece of work that would have made his scientific name. In three successive years, Thompson applied for fellowships at Trinity College that would have allowed him to continue studying at Cambridge, but like his father he was never successful. Despite his loner’s sensibilities, Thompson craved the scientific establishment’s recognition, and its failure to arrive hurt him. “I came to [Trinity] in exultation,” he wrote toward the end of his life. “I left it in deepest disappointment.”

A Lean and Hungry Town

Thompson may have felt snubbed at Cambridge, but his professors gave him glowing testimonials. He also got a recommendation from his uncle, Arthur Gamgee, sometimes credited as the first biochemist for his work on the chemical composition of the body and the chemical changes that accompany disease. Armed with these references, Thompson got a job back in Scotland in 1884, at the newly established University College of Dundee. Dundee had grown rich on the textiles industry, but had also grown grim—it had more money than class, and more slums than money: “An east-windy... lean and hungry town,” Thompson wrote. It was soon to get much leaner, as the textile industry collapsed in the face of competition from India. But Dundee also had a zeal for self-improvement, and so in 1883 the college was founded, with an emphasis on the new sciences and a faculty of bright young professors to teach them. By now his father’s ideas about education were more widely accepted, and Thompson junior lectured to equal numbers of women and men.

Thompson threw himself into Dundee life, getting involved in the college’s administration and politics, setting up its zoology museum, and doing philanthropic work in the town. Thompson’s speciality was marine biology—he loved the sea and was proud of his family’s
nautical heritage. He made regular visits to Dundee’s docks in search of specimens fresh from fishing boats and whaling ships, and built up an outstanding collection of arctic specimens in the college museum. In 1896 this work attracted the government’s attention. For 50 years the powers with interests in the North Pacific—the United States, Russia, and Great Britain, via her colony Canada—had wrangled over the regulation of the fur seal hunt. The same issues that exercise managers of commercially exploited species today were just as contentious then: how many animals could be taken, when and where, and the extent of poaching. The British foreign office commissioned Thompson to study the seal population to assess whether the hunt was, in today’s jargon, sustainable. Besides his marine expertise, he had made a good impression on the foreign secretary’s nephew while at Cambridge.

Thompson sailed to New York in May and traveled overland to Seattle, where he met up with an American team charged with the same mission. They boarded a boat north to the Aleutian Islands, which stretch out into the Pacific off Alaska. Thompson collected specimens of every species that crossed his path, to swell the collection in Dundee. Once he reached the seal colonies, he did all the things that a good conservation biologist should: counting the population and trying to estimate the natural levels and causes of pup mortality.

He also saw seals driven in their hundreds from breeding rookeries to killing grounds. The drive sounds a strange sight, but Thompson’s account of it is unperturbed:

The seals certainly puffed and blew and sweated and steamed; they stopped every now and then to rest . . . but after a moment they went on briskly. The signs of distress were less painful than I have often witnessed in a flock of sheep on a hot and dusty road, and I have seen drovers show less regard for the comfort of their sheep.

The drive began at 2:00 in the morning, and by 6:00, a herd of nearly 2,000 seals had reached the killing grounds, where teams of men with clubs waited.

The men employed were clean, skilful and vigorous. A single blow, or two at most, dispatched each seal, and I saw no failure of aim, even in the confused mass of seals tumbled pell-mell over one another. They showed no signs of terror; the survivors of each batch [only about half of the driven seals were killed: those either too young or too old were released] made
quickly for the water, and were already swimming homeward as the next batch were being slain. . . Two younger lads went round plunging a knife into the heart of any seal that still breathed; five (ripers) proceeded to slit the skins down the belly and around the neck and paws, after which the rest flayed the carcasses. The work of skinning nearly kept pace with that of killing. I could not detect in the whole process either intentional or accidental cruelty. . . The killing was concluded by about 10 o'clock, an interval for breakfast intervening.

The next year he went to Alaska again, this time going east via Ceylon and Japan. In his final report to the Bering Sea Commission, Thompson concluded that the seal hunt was sustainable at its present level but that there was no room for complacency: "We may hope for a perpetuation of the present numbers; we cannot count on an increase." He also noted that the killing of other marine mammals—whales, walruses, and sea otters—was less well regulated and posed a greater threat to those species' survival.

The experience gave Thompson a taste for fisheries research, and for international collaborations. In 1898 he joined the fisheries board of Scotland, which was to become a lifelong commitment, and from 1902 onward he represented Scotland on the newly formed International Council for the Exploration of the Sea, lobbying the British government to support the fledgling body. All the while he kept up his classical studies. In 1901 he married Maureen Drury, his step-mother's niece. Over the next nine years, his three daughters Ruth, Molly, and Barbara were born.

But this life left Thompson little time for his own research, and his work on applied problems cut little ice with the people who gave out jobs. "You must show that the waters of the Pacific have not washed the science out of your composition," wrote an old Cambridge friend. Through the 1890s, Thompson applied for positions at more eminent institutions in London, Edinburgh, and Glasgow, but failed to get any of them. On the other hand, he applied for and won a professorship in Aberdeen but turned it down; he clearly wanted to work on his own terms, even if it hindered his progress up the greasy pole of academia. Other researchers saw him as an unproductive oddball in two fields; his papers on classical scholarship were rejected just as often as his biology ones.

Besides his political failings, Thompson slowed his advancement by taking a near-heretical view of biological science. In the early twentieth century, biologists, reveling in—or reeling from—the triumph of Darwinism, tended to use evolution as a catch-all answer to biology's "why?" questions. Why was any animal the way it was? Because natural selection favored it—never mind how. Biology was concerned with stories, not causes: Animals were seen as archives of evolution, and biologists' main task was to use specimens' anatomy to work out their history. Then, by comparison with other species, researchers could assign each creature its place on life's family tree. As the British immunologist Peter Medawar later wrote, biologists "accepted the contemporary and far from adequate form of Darwinism in much the way that nicely brought up people accept their religion, that is, in a manner that contrives to be both tenacious and perfunctory." Most zoologists were not much interested in how animals got to be the way they were, in either the long-term evolutionary sense or the short-term developmental sense. Nor were they interested in how animals worked; rather than ask why a bone took a particular form, they just wanted to compare it with the same bone in different species. But most of the striking advances in comparative anatomy were already decades old. Evolutionary biology was snoozing.

Perhaps this is why Thompson came to take a dim view of natural selection and genetics. He was interested in causes, thinking that when we see some feature in an organism, we should seek some underlying force that has brought the trait about. Simply to invoke heredity, as many biologists then did—for example, in the popular idea known as "ontogeny recapitulates phylogeny," which hypothesized that the process of an animal's embryological development re-enacted its evolutionary ancestry—seemed uselessly vague. "I should be [equally] at a loss to disprove the hypothesis that the Moon was made of green cheese," Thompson wrote of the notion that evolution could explain how living things arrived at their present forms. He was no creationist: He granted that natural selection could weed out the unfit, but doubted its power as a creative force, able to explain why life took one form and not another. He also thought that physical similarities were a poor guide to shared ancestry—another position unlikely to endear him to
his peers, since that is what they spent much of their time doing. The disenchantment began in Cambridge, where he could never summon up much interest in the lineages or relationships of species. His professors advised him to keep his thoughts on evolution to himself: “You might think these things, but you mustn’t say them,” one warned.

Isolated in Dundee, however, Thompson could give his originality its head and, untroubled by career success, work on what he liked. In 1894 he presented a paper to the British Association meeting in Oxford titled “Some Difficulties of Darwinism,” in which he expressed doubt that, among other things, the vibrant colors of hummingbirds could come about through a dour struggle for existence. Thompson, in contrast, saw the plumage as the product of a benign environment. The hummingbird’s livery, he suggested, was the product of “laws of growth,” operating unchecked by natural selection. He also sought to banish natural selection from the shape of birds’ eggs, arguing that the narrow, pointed eggs of the guillemot, a seabird that nests on cliff ledges, were formed by pressure from muscles in the mother’s oviduct. This contrasted with, although it does not contradict, the evolutionary explanation that this shape gives the eggs a tight turning circle and stops them from rolling off their ledge. One of Thompson’s old Cambridge professors was in the chair. “He did not hide his impatience and disapproval,” Thompson later recalled. “There were no difficulties in Darwinism, either to him or any sensible man in those days.” In truth, Thompson’s notions about evolution and natural selection have not aged well. But his efforts to formulate new laws to put in the place of natural selection took him down many fruitful paths. In the process he pioneered a different type of biological thinking and a new type of biological explanation.

Unsuspected Wonders

The seeds of mathematical and physical thinking germinated in Thompson’s mind in the late 1880s. In October 1889 he wrote to Mary Lily Walker, a former student: “I have taken to Mathematics, and believe I have discovered some unsuspected wonders in regard to the Spirals of the Foraminifera!”

Foraminifera are microscopic sea creatures with intricate and beautiful shells. Thompson did not say what he had discovered, but I suspect he had noticed that many foraminifera have shells that take the form of an equiangular, or logarithmic, spiral. In this shape each whorl is broader than its predecessor, but the ratio of breadths remains constant. In other words, the shell is a coiled cone. Traveling outward from the cone’s apex at the center of the shell, the tube becomes progressively broader, but always at the same rate. This spiral was to lie at the heart of Thompson’s thinking for the rest of his life. Into his seventies and eighties, he was still writing to biologists and engineers, seeking to understand how the shells of sea snails and the horns of antelopes and narwhals, which are also equiangular spirals, came about.

Thompson began to investigate other marine creatures and found that mathematics could describe their form too. In some sponges, small bony particles called spicules make a scaffold for the animal’s soft tissue. Thompson began to think that the form of these spicules might be determined by the animal laying down mineral crystals in gaps between its cells. Three spherical cells in contact would, like soap bubbles, produce a three-rayed crystal with equal angles of 120° between its arms, like the center of the Mercedes-Benz logo. In 1890 he shared these observations with a student, George Petrie, who was astounded: “I became aware that mathematics may be applied to give precision to biological observations and thus to open up a fascinating vista of speculations,” he wrote. Physical forces gave Thompson an alternative to heredity as an explanation of the form of animals. He decided that physics was all that was needed to explain spicules’ shape, and that similarities between species probably reflected shared physical conditions, not shared ancestry.

In 1894, the same year he told the British Association meeting of his concerns over Darwinism, his speculations about laws of growth, and his belief in the power of physical forces to shape living forms, Thompson wrote to Michael Foster, a comparative physiologist who had taught him at Cambridge, about this line of reasoning. Foster, one of the most powerful zoologists in Britain, was less than enthused. “I confess I am not very much attracted by this line of work, and doubt if it’s likely to be fruitful,” he replied. “If the form is constant in a group—
it does not matter how the form is brought about.” It seems bizarre now, but Foster was only interested in using the shape of sponges’ spicules as a tool for recognizing species and assigning them to different groups. He seems to have seen any investigation of how the shape of a spicule came about, or why, as irrelevant and possibly dangerous. “Does your result wholly destroy the diagnostic value of the spicules?” he wrote. Thompson published nothing else in this line until a paper in the scientific journal Nature in 1908, which revisited his thoughts on the shapes of eggs. In Dundee he discussed what he called his heresies with assistants but was unwilling to publish, saying “everyone will say they have read it all before.” Maybe he also feared further ostracism.

**Aristotle’s Disciple**

Yet as he entered his sixth decade, Thompson’s career took flight. In 1910, eight years after his father’s death, he finally completed the translation of *Historium Animalium* that the two had begun decades earlier. It remains the standard version of the work and will always be so, as there is unlikely to be another naturalist who knows as much Greek nor a classicist as expert in zoology. Thompson thought Aristotle the greatest of all biologists: “No man has ever looked upon our science with a more far-seeing and comprehending eye,” he told the British Association a year later. In 1911, Cambridge awarded him a doctorate, in letters rather than science, for the Aristotle translation and another work published 15 years earlier, *The Glossary of Greek Birds*, a gazetteer of matters ornithological in Greek literature that Thompson called “the apple of my eye.”

D’Arcy Thompson’s later achievements make me wonder whether his earlier outsider status was largely self-imposed and that at some point he simply decided to stop shunning the brethren and embrace them. In his fifties he also began to pursue his thoughts on physics, mathematics, and biology in earnest. The aforementioned 1911 talk at the British Association’s meeting in Portsmouth was delivered from his position as president of the association’s zoological section. After the encomium to Aristotle, Thompson went on to outline his view of “the greater problems of biology.”

The foremost of these problems was vitalism. “The hypothesis of a Vital Principle, or vital element,” Thompson told his audience, “is the greatest question for the biologist of all.” The debate had been given new form by studies of cells, embryology, and reproduction—processes that seemed almost magical, and certainly far removed from physics and chemistry. Yet just as a cellular view of life had revealed that zoologists, botanists, and physiologists were all studying essentially the same thing, Thompson argued that still deeper investigation would dissolve the distinction between biology, chemistry, and physics. Only then would we have a true understanding of biology.

Thompson thought that some sciences were more scientific than others. Chemistry outranked biology and was in turn topped by physics, with mathematics standing at the pinnacle. The problem with vitalism—and heredity—was the belief that the explanations for biological phenomena could be found in biology. Instead, biologists should go up the chain of explanations, to chemistry and beyond. They had neglected the physical sciences to their detriment. Why invoke vitalism when so many of the forms in the living world can be explained by simple physical principles? The physics of surface tension, Thompson noted, explain why raindrops are spherical, because this shape has the minimal surface area. Likewise, he argued, surface tension could explain the shape of amoeboid cells, or the spread of sticky droplets over a spider’s web. “Has the biologist,” Thompson asked, “fully recognized . . . that the physicist may, and must, be his guide and teacher in many matters regarding organic form? . . . In many of the simpler cases the facts are so well explained by surface tension, that it is difficult to find a place for a conflicting, much less an overriding, force.” Vitalism, in short, was unnecessary.

Around this time, Thompson agreed to write up his thesis in what he called a “little one-shilling or two-shillings-and-sixpence book for the Cambridge University Press on ‘Form and Growth’.” But the work grew, and any prospect of publication disappeared into the distance, as the edifice that had begun as a simple chapel grew into a cathedral. Thompson hinted at what he was up to in December 1914, in a paper presented to the Royal Society of Edinburgh titled “Morphology and Mathematics.” Again, he began by blowing the trumpet for bringing biology under physics’ umbrella. Biological forms, he argued, were a
subset of those seen in nature, which were themselves a subset of all those theoretically—that is, mathematically—possible. Biologists should stop worrying about how a natural form, such as a shell, differed from an abstract spiral and instead learn from the similarities. Then they would see how mathematics would lead them from description, to analysis, to generalities.

But, he conceded, most of the forms in living organisms were far too complex to yield their secrets to such simple analytical tools. This, however, did not exclude the use of mathematics to compare different shapes. Adapting a technique developed by renaissance artists, particularly Albrecht Dürer, he laid coordinate grids over pictures of animals, or shells, or bones and showed how distorting them in a regular fashion could produce the forms of other related species, like the same landmass shown in two different cartographical projections. (Thompson would demonstrate this principle to children by drawing a normally proportioned dog on a piece of rubber and then stretching it to produce a dachshund.) Again, mathematics showed a path out of the forest of details: Instead of a separate rule to create every difference between two species—a round body versus a torpedo shape, a short snout versus a pointed one, a sloping forehead versus a high brow—you only needed one.

The work was well received—"profoundly interesting," said one biologist—and it may have been the decisive factor in Thompson's election to fellow of the Royal Society of London the following year. This is the highest honor that British scientists can grant one another—not exactly the mark of a crank. It suggests that Thompson's fellow biologists never held him in the low esteem he had assumed. In 1917, Thompson finally escaped Dundee, when the college merged with the nearby university at St. Andrews, and he moved to take the zoology professorship there. He conceded that St. Andrews was, like Dundee, "a cold grey city by the Northern Sea." But the intellectual climate was more congenial. "A town of scholars these five hundred years," it churned out learning like Dundee had once produced cloth. The same year his unified theory of biology, mathematics, and physics was published—he had finished it in 1915, but the First World War had delayed its publication. The book was called On Growth and Form. Presenting

D'Arcy Thompson's transformation grids aimed to show how a simple mathematical operation could turn a parrotfish (top left) into an angelfish (top right), or Polyprion (bottom left) into a big-eye (bottom right).
Credit: Reprinted with the permission of Cambridge University.

his philosophy as a tome, rather than a steady trickle of papers, might have been another bad career move, but it secured his place in posterity.

On Growth and Form

If the Portsmouth and Edinburgh papers were sonatas, On Growth and Form was a symphony. But all three had the same theme: the path to understanding living things leads through mathematical analysis. Surveying physics and chemistry, it struck Thompson that as these disciplines had become more precise and powerful, they had also become more mathematical. Mathematics, it seemed, was at the heart of good
scientific explanation. In this regard, biology lagged far behind the other sciences and was therefore less able to proclaim itself a true science.

And yet there was plenty of room for mathematics in biology. As he turned his eye to the animal kingdom, Thompson noticed that nature dealt in the same regular forms as the Greek geometers: cylinders, hexagons, triangles. He devoted several chapters to his beloved equiangular spiral, revealing it in the shells of snails and nautilus, in horns, claws, and teeth. He noticed that many of these forms could also be found in inanimate nature, such as waves, hills, clouds, and snowflakes. High-speed photography revealed that a drop of water falling into a puddle made a splash that looked a lot like the polyp of the hydra, a marine invertebrate related to sea anemones. The curly, turbulent eddies that jets of oil or ink make when they flow into water looked like the canopy of a jellyfish. The cells in a dragonfly’s wing looked like a film of soap bubbles. Thompson wanted to convince his readers that, in contrast to vitalist philosophy, the laws of physics apply to living organisms and that life does nothing that breaks these laws. What’s more, just as physics explained why a wave or snowflake took a particular shape, so too could it explain why an animal did, without recourse to natural selection. Biological form, he reasoned, could be the consequence of physical forces acting on living matter, just as other natural forms could come about through these forces acting on water and rock. In this line of his thinking, Thompson was also pioneering the use of models in biology. He outlined a set of rules and conditions and then saw what the consequences of those rules would be for living matter. These thought experiments produced results that closely matched living structures, convincing Thompson that he understood the underlying principles.

Thompson also pointed out the similarities between natural and artificial structures. An architect designing a bridge will study the loads it must carry, and the gales it will have to withstand, before deciding where to put struts and cables. Likewise the internal structure of a bone is a striking match to the stresses it will endure in life: Its tough outer layer is thicker in the middle than at either end, as fracturing is more likely here, and, like a girder, it contains a network of supports that mimic the forces placed on it. An organism, said Thompson, was “a diagram of forces.” Where previous biologists had taken it for granted that organisms were well adapted to their environment, Thompson demonstrated what this meant.

The third strand of Thompson’s thinking—and the driving force behind the Theory of Transformations unveiled in Edinburgh and expanded on in *On Growth and Form*—was that mathematical thinking could reveal simple principles underlying the diversity of natural forms. You do not need to assume that a sponge somehow intervenes to determine every aspect of its spicules, any more than a snowflake controls its shape. Both are explained by the rules that describe how minerals aggregate to form crystals. A snail doesn’t have a design in mind for its shell; it just adds material to it as it grows, producing the spiral. And small changes in the geometry of this process can produce the many types of shell—thin and fat, simple and intricate, round and spindly—seen in living snails.

Thompson’s analyses of living forms, and the comparisons he drew with the design of man-made forms, were visionary. He was, however, stronger on form than on growth, and his advocacy of physical forces as the prime movers in animal development was less successful. For example, he thought that bones develop their networks of struts and supports in response to the physical forces acting on them, rather than by following a genetic program. In fact, a bone will develop its usual reinforcements even if it is transplanted to another part of the body, where it experiences a different set of forces.

His mistrust of evolution led him astray. Bones develop the way they do because natural selection has favored a developmental path that makes bones that can cope with the stresses of life, not because those stresses control the development of bone. His blind spot regarding genetics was at least the equal of any of the earlier comparative anatomists regarding physics. He simply ignored it, dismissing the question of what the units of heredity might be, and how they might be ordered and transmitted, as uninteresting. In his science, as in his career, he could never be bothered to plough anyone else’s furrow, and he refused to adapt his thinking. In a 1923 letter 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.” Maintaining this position as the century progressed and genetics came to dominate biology must have called on all of Thompson’s substantial reserves of bloody-mindedness.

It is difficult to work out what Thompson thought drove growth, but he seems to have believed that the development of animals and plants tended to produce structures that were mathematically harmonious or, at least, that living matter naturally assumed such forms and that elegant mathematics was synonymous with biological adaptation. He replaced the vitalist life force, and Darwin’s struggle for existence, with a striving for physical flawlessness: “The perfection of mathematical beauty is such that whatsoever is most beautiful and regular is also found to be most useful and excellent.”

D’Arcy was struck, for example, by the ubiquity of spiral shells across the animal kingdom—in molluscs, worms, foraminifera:

These forms present themselves with but little relation to the character of the creature by which they are produced... We find the same forms, or forms which are mathematically identical, repeating themselves in all periods of the world’s geological history, and we see them mixed up, one with another, irrespective of climate or local conditions, in the depths and on the shores of every sea. It is hard indeed (to my mind) to see in such a case as this where Natural Selection necessarily enters in, or to admit that it has had any share whatsoever in the production of these varied conformations.

One might as well invoke natural selection to answer why one type of cloud was common and another rare.

Nowadays, this seems like a failure of imagination. Biologists have no trouble coming up with reasons why natural selection might explain any aspect of anatomy or behavior. But while Thompson’s ideas about how evolution works were off the mark, his critiques prefigured many of the issues that exercised evolutionary biologists through the twentieth century. Spiral shells, for example, show convergent evolution, where unrelated animals come up with similar solutions to the same problem—containing a growing body within a shell. The commonness of spiral shells across species and through geological time also hints at evolutionary constraints—the idea that the forms that can evolve are limited by an organism’s history and developmental flexibility. Thompson also took issue with the idea that evolution meant progress—a smooth path toward better organisms. If unchanging physical forces controlled animal form, this need not have been the case: “I for one imagine that a pterodactyl flew no less well than an albatross.” Now, few think that the giant prehistoric reptiles were stupid, or clumsy, or poorly adapted to their world: Instead we stress the part that chance, in the form of a meteorite, may have played in their demise.

On Growth and Form made Thompson famous. Nature compared it to one of Darwin’s books, calling it “substantial and stately.” The Observer newspaper called Thompson “a ripe philosopher and a scholarly historian, possessed of artistic and literary gifts of no mean order.” His peers were equally impressed. One Cambridge zoologist wrote to thank D’Arcy: “That the form of animals and plants is not to be regarded as due to a hopelessly complex series of biological factors, but shows the operation of comparatively simple and harmonious physical laws, is, I think, a very great contribution to biology.”

Thompson embraced his recognition. In 1918 he gave the Royal Institution’s Christmas lectures for children, on marine biology. And throughout his life he seems to have jumped at any chance for a trip that came along—then, as now, one of the perks of academic life. He gave lectures across Europe and in South Africa and the United States, collecting honorary degrees and society medals as he went, and journeyed to Soviet Russia as part of a Royal Society delegation. He also won acclaim as a classical scholar, serving as president of the Classical Association of Great Britain in 1929. In 1937 he represented the Edinburgh Royal Society at King George VI’s coronation, and was knighted later that year. He gave radio broadcasts, and produced a stream of pieces on every topic for scholarly journals, newspapers, and magazines. With his love of dancing, taste for Savile Row suits, and habit of walking around St. Andrews with a parrot on his shoulder, it’s hard to avoid the conclusion that inside Thompson’s lonely soul an inveterate show-off had been itching to get out.

Wartime shortages limited the first printing of On Growth and Form to 1,000 copies. Thompson was keen for a new print run but wanted a second edition rather than just a reprinting: “I wish to goodness the first edition would run out, and let me bring out a new one. I
have a good deal to correct, and more to add." The Cambridge University Press agreed, writing to him in May 1923, when stocks of the first edition were running low: "[W]e will be glad to put in hand a new impression of the work, provided that the corrections you wish to make are few in number." Given D'Arcy's perfectionism and the work's history—the press had contracted for a book of 144 pages; the final work was more than three times this length and arrived several years late—this smacks of hope triumphing over experience.

By October 1929 the press's letters had a plaintive tone: "For the past few years we have announced a new edition as being in preparation, and we have eager inquiries from would-be purchasers from time to time." Thompson delivered the first two chapters of the revised edition in August 1939.

By 1941 his publishers were trying threats: "I must warn you that you have already slightly exceeded the correction allowance specified in Clause (6) of the agreement." The second edition was completed in 1942—it seems to have taken a world war for Thompson to curtail his travels and take to his desk—by which time first editions were changing hands for 10 times the original cover price of 21 shillings. The updated version, in which Thompson struggles to show that he is at least aware of the intervening decades of biology but does not really care to incorporate new developments into his theories, was two volumes and 1,100 pages long—almost twice the length of the first edition. Although well reviewed at the time, it is now thought to be not as good.

After the war ended Thompson, despite being in his eighties, was quick to take to his travels again. In January 1947 he journeyed to India as a representative of the Royal Society. In a typical piece of showmanship, he lectured in Delhi on the mechanical structure of bird skeletons with a live chicken under his arm. But the long journey broke his health, and he had to leave India earlier than he had intended. His health improved a bit when he got home, but the spring of 1947 was unseasonably cold, and Thompson came down with pneumonia. He recovered again in the summer and oversaw publication of A Glossary of Greek Fishes, a companion piece to the book on birds published half a century earlier. But pneumonia and other ailments returned in the autumn, and by the winter he was too weak to visit the university. From then on his health gradually declined. Thompson had a sanguine attitude toward old age—unsurprising in one who should be the patron saint of late starters—but as he became an invalid this turned to despair: "I long for release," he wrote on June 9, 1948. He died at home 12 days later. His combined tenure at Dundee and St. Andrews had lasted a record-breaking, if inadvertent, 64 years.

The Last Victorian

D'Arcy Thompson was the last Victorian scientist, in his schooling and classical roots, breadth of knowledge, ferocious work ethic—he would retire to his study at 10:00 each night for two more hours of reading, writing, and thinking before bed—courteous manners, starched collars, voluminous beard, and penchant for a daily cold bath. As Peter Medawar has commented, On Growth and Form is a work of natural philosophy rather than modern science. But this was a tactical choice on Thompson's part, as much as a philosophical one. His work on fisheries and oceanography shows that he was perfectly capable of getting his hands dirty in the field and the lab. Yet On Growth and Form contains few new observations, and Thompson conducted no significant experiments in this, the enduring thread of his scientific career. When he turned his attention to physics and mathematics in biology, Thompson decided that there were already quite enough facts available—what was needed was a synthesizer to tease out the threads of an argument from the disparate work of other researchers. His polylectic background in everything from engineering to Ancient Greek, and his linguistic gifts, which included French and Italian, made him well equipped for the task.

Thompson's unique qualities, unusual career path, and individualistic approach make his science unrepeatable. As a consequence, his place in biology is both marginal and pivotal. His use of mathematics was an inspiring example, but the techniques he favored, based mainly on classical geometry, never took off among his peers. Instead, modern biologists use calculus more often than any other technique. And many biologists remain untroubled by mathematics—today, you can still flick through whole issues of journals in molecular genetics, immu-
ology, and developmental biology without seeing an equation. Thompson's distaste for genetics meant he never engaged with the most successful area of twentieth-century biology—indeed, genetics has filled the role in which Thompson sought to cast physics, by showing that the diversity of living species springs from the same underlying processes. Cell biology and molecular biology also have pursued an understanding of living things by ferreting out the details, whereas Thompson thought such details risked obscuring deeper generalities. He rarely went beyond description to explanation, and the two may have been blurred in his mind. Thompson's favorite way of making a point was through visual analogy; the historian of science Evelyn Fox Keller has pointed out that, for a book about mathematics, *On Growth and Form* contains surprisingly few equations. His transformational grids, the most original part of his work, never took off. It's hard to see how to pursue the method beyond drawing a striking picture, and the analyses required formidable computing power (now that this has arrived, researchers have developed some ways to analyze biological shapes that have a lot in common with Thompson's transformation grids). And some of his ideas were just plain wrong.

All this makes Thompson seem antique, and it's true that as time passes his lines of thought become harder to follow. There are trivial reasons for this: *On Growth and Form* is dense with untranslated quotes in Greek, Latin, and modern European languages. But even with translations, the increasing narrowness of modern scientific training and expertise makes Thompson's all-embracing approach hard for modern readers to interpret. Stephen Jay Gould, who from his introduction to the current edition of *On Growth and Form* seems to have seen himself as a contemporary equivalent of Thompson—and with some justification, as both had wide interests, elegant prose styles, and idiosyncratic views on evolution—wrote that his colleagues saw the book as "an unusable masterpiece."

On the other hand, the debate around vitalism was still alive in Thompson's day, particularly among zoologists—his work helped put an end to it. No serious scientist now believes that living things are exempt from the laws of physics or made from different stuff than dead matter. And although Thompson's mathematics may have gone out of fashion, mathematical models are now used to study everything from enzymes, to bird flight, to the waxing and waning of populations, to where animals should feed, and whether they will evolve unwieldy tails or dazzling, hummingbird-like plumage. Mathematics has allowed biologists to go beyond qualitative verbal arguments to making precise quantitative measurements and predictions and to develop rigorous theories.

Most importantly, Thompson pioneered a new way of thinking about life and a new type of explanation in biology. Underneath the evolutionary eccentricities, *On Growth and Form* challenges biologists to ask why an organism takes the form it does and to look at biology in terms of mechanisms and solutions. Ironically, Thompson's work has helped us understand how natural selection works: Where he talked about an animal being a diagram of forces, biologists now talk about living things being shaped by selection pressures.

And because he made no distinction between the physical and biological worlds, Thompson was also able to pursue this line of thought to what were, in his time, some unusual places. For example, he thought about anatomy at the molecular level and drew links between the shapes of molecules and the shapes of biological structures. Looked at in this light, James Watson and Francis Crick's model of the structure of DNA—the all-time great piece of molecular anatomy—becomes a rather Thompsonian piece of work. Those two were trying to find a biological form consistent with physical forces, an arrangement of atoms and molecules that would be stable. In the process they arrived at a structure that also demonstrates how heredity might work, leaping from form to function. And like Thompson, they arrived at their conclusions by theorizing and modeling, rather than doing experiments—Thompson used cardboard models to try and understand the geometry of cell shapes and bee cells—and they were guided by a belief that the structure of DNA would be aesthetically appealing. As Watson wrote, the double helix was "too pretty not to be true."

But perhaps the main reason that *On Growth and Form* is still in print is that it is simply a beautiful book. Thompson considered writing his principal talent: "The little gift of writing English," he wrote, "is, speaking honestly and seriously, the one thing I am a bit proud and
vain of." The spider's web he mentioned in Portsmouth he described as "bespangled with dew, and its threads bestrung with pearls innumerable." Other parts of his writing have a biblical tone:

Not only the movements of the heavenly host must be determined by observation and elucidated by mathematics, but whatsoever else can be expressed by number and defined by natural law. This is the teaching of Plato and Pythagoras, and the message of Greek wisdom to mankind.

Medawar—himself a superb writer—thought the book "beyond comparison the finest work of literature in all the annals of science that have been recorded in the English tongue."

On Growth and Form should appeal to anyone interested in ideas who appreciates seeing a fine writer making an effort to persuade them. Its status as art has won it a special place in biologists' hearts: They are proud that their discipline has produced such a work of literature, and even its wrongness and eccentricities seem to only add to its charm. In the 1917 edition, for example, Thompson wrote sympathetically about panspermia—the idea that life has traveled between planets and star systems. Propelled by the Aurora, he noted, a microbe could get from Earth to Jupiter in 80 days and reach Alpha Centauri in 3,000 years. It is the sort of book that inspiring teachers press on their students, who then become teachers or researchers themselves and press the book on the next generation of students. From the start, its influence has stretched beyond biologists to engineers and architects, artists, and mathematicians. Soon after the first edition came out, there were inquiries from The Builder, the Journal of Decorative Art, and the Mathematical Bulletin. While writing this chapter in autumn 2004, I visited an exhibition in London of work by the Mexican artist Gabriel Orozco, whose sculpture Black Kites features a grid of distorted squares mapped out across a human skull, very much like a Thompsonian transformation. Around the same time, the German architect Frei Otto won the Royal Institute of British Architects' Royal Gold Medal, architecture's most prestigious award. Otto, whose projects include the roof of the Munich stadium used for the 1972 Olympics, pioneered lightweight building using high-tech materials. He took inspiration from cobwebs, bird bones, and crab shells in making his buildings light, economical, and strong, giving them the minimalist elegance of natural forms.

But science is not just about elegance, Aristotle, and the life of the mind. It is also grunt work—prodding, dissecting, and measuring. And while Thompson strained to hear the music of the spheres in the spiral of a seashell, a group of his more experimentally minded contemporaries were attempting to understand living energy by analyzing the chemicals in dog turds, wrapping people in brown paper, and painting stripes on cows.