Turning old facts into new knowledge:
D’Arcy Thompson’s “On Growth and Form” a century on

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This book of mine has little need of preface, for indeed it is ‘all preface’ from beginning to end.
D’Arcy Thompson, in the preface to On Growth and Form

This year marks the centenary of the publication of D’Arcy Wentworth Thompson’s prophetic volume on biological morphology entitled “On Growth and Form”. We will mention it so often in what follows that we will abbreviate it simply as OGF. This magisterial tome is significant for several reasons. Not only can it be regarded as marking the dawn of an age in which biology can be subject to the same kind of mathematical analysis as physics and chemistry before it, but in some sense it also draws a historical line between a medieval vitalist spirit of examining biological problems and a more modern viewpoint, in which living organisms are subject to the same scientific laws as those of all inorganic matter. It further provides an antidote to the reductionist strategy of the chemist, who looks for detailed process, rather seeking unifying themes from the fundamental laws of mathematics and physics to describe and explain the commonalities that link our understanding of different kinds of living structures. And if that were not enough, it includes an assembly of no fewer than 408 spectacular illustrations, some examples of which are reproduced in Fig.1.

All this has contributed to propelling a “trade” volume, authored by an archetypical ivory tower intellectual, with an initial run of just 500 copies, to such cult status that for the last 70 years it has never been out of print.

This anniversary provides an excuse both to look back and to look forward in the spirit of D’Arcy Thompson. We shall look back at progress over the last hundred years in theoretical approaches to developmental biology. And just a little, we shall try to peek at how the 21st century biological community can consummate some of the unrealised and unspoken ambitions of the 19th century naturalists.

Thompson had academic interests of an extraordinary breadth. Educated in Natural Sciences and other subjects at Trinity College Cambridge, he was by 24 already professor of biology at University College Dundee. There he remained until 1917, when he transferred to a chair at the University of St Andrews, where he continued in post until his death in 1948 at the age of 88. On the way he accumulated honours galore, including fellowships of the Royal Societies of Edinburgh (1885) and of London (1916), and a knighthood
(1937). His publication record stretched over almost seventy years, between 1879 and 1945, comprising some 300 items, some concerned with biology and natural history, some with the classics, along with ventures into the application of mathematics to the biological sciences (ultimately leading to OGF), for which he is justly famous.

The original 1917 version of OGF [1] (here OGF1) comprised a ‘mere’ 793 pages, concerning learned aspects of mathematics and physics as applied to biology. The initial limited print run of 500 copies would only be exhausted in 1922, at which point a second edition was requested. But Thompson was a busy man, and a perfectionist, so the second revised edition, comprising an even bulkier 1116 pages, did not appear until 1942 [2] (here OGF2). Both editions are freely available on the web.

A 1952 article in *Scientific American* [3] by the up-and-coming Princeton biologist John Tyler Bonner opines that it is “a depository of original ideas that have influenced developmental biology”, and that it is “a work of literature whose style has few peers in the field of biology”. Because of this, avers Bonner, it “is frequently condemned or dismissed by experimental scientists”. So Bonner aspired to produce a version of OGF, which could appeal to workaday experimental biologists. Thus the abridged edition appeared in 1961 [4], edited by Bonner, containing a digestible summary of only 346 pages. This is the edition normally used by contemporary scholars.

As regards the content of OGF, we have space only to draw attention to some main themes that infuse the work as a whole. Let us start not so much with what is present but with what is, to the modern critical eye, absent. A century and a half on from Darwin, almost all biologists now regard the Theory of Evolution by
Natural Selection, and the genetics that describes how the process works, at both the microscopic and macroscopic levels – the so-called Neo-Darwinian Synthesis [5, 6] – as central organisational tools for biological understanding. However, this was not generally the case in 1917, and it was certainly not the case for Thompson. It was not so much that he was against Natural Selection. Rather he was sceptical that this was the whole story. In 1894, he published a note in Nature entitled “Some Difficulties in Darwinism” [7]. By 1917 his position had hardened and OGF elaborates his arguments further. Darwin and Wallace had ascribed, to common descent alone, the origins of the homologies enabling the classification of organisms into a “Tree of Life”. But Thompson disagreed, stating (OGF1, p251) that

… this great generalisation is apt in my opinion to carry us too far.

And as for the young science of genetics, there is nothing at all in OGF. Yet, in the years over which OGF was in preparation (roughly 1905-1915), ideas of genetics were recent, current and very much in vogue [8]. Rather than think about populations (and, of course, not knowing any molecular genetics at all), Thompson concentrated on the mysteries of building individuals: what particularly interested him was morphology – a term introduced to the biological sciences by the writer Johann Wolfgang Goethe in 1790, to describe the study of plant and animal shapes – and the role of common physical forces in the shaping of biological forms [9].

Although ostensibly a treatise on the role of physics in biology, and the utility of mathematics in understanding it, much of the applicable mathematics already available in 1917 is absent from OGF. In a critique of Thompson’s approach to growth and form, the distinguished popular evolutionist Stephen J. Gould pointed out [10] that Thompson’s mathematics has:

a curious ring…(since) we find none of the differential equations and mathematical statistics that adorn modern work [e.g. in] ecology or population genetics … we read instead of the Mirdali angle, the logarithmic spiral and the golden ratio. Numbers rarely enter equations; rather they exemplify geometry.

On this basis, Gould characterises Thompson as a Greek mathematician with 20th Century material and insights, commenting that this reflects the synthesis of his two lives: eminent classicist and … zoologist.

Indeed, the very title On Growth and Form brings together these two aspects of his physico-mathematical discourse, form being addressed from the Pythagorean and Platonic viewpoint, while Newtonian mechanics is adopted for his discussion of growth. To modern eyes, these two elements of developmental biology do not sit comfortably together without further mathematical elaboration, much of which was available in 1917 – for example, the tools of differential and integral calculus, and topology, that played so central a part in the physical theories that were being developed around that time. In his defence, Thompson does comment (though not in the 1917 edition!), that (OGF2, pp10-11)

He [the morphologist] may come to realise that there is no branch of mathematics, however abstract, which may not someday be applied to phenomena of the real world…

Yet this belief is not practised in OGF. To Thompson, this was a philosophical, rather than a practical, truth.
The 1942 edition, though much expanded, still retained the opening comment (from the 1917 edition) that the whole work should be considered merely as a preface. This reflects the fact that there was nothing fundamentally new as compared to the first edition, but that the additional space was filled by many more examples illustrating the messages Thompson wished to convey. To many readers this meant that the new edition was harder to read, and the fundamental ideas were obscured by a surfeit of new material, which collectively provided no new unifying principles, just a treasure trove of examples. Hence the reviews were mixed. For example, in the *Journal of Physiological Zoology*, J. W. Buchanan [11] compliments the beauty of the prose and the learning of the author, but adds:

The reviewer regrets that he is compelled to raise some more or less important criticisms of this long and exquisitely prepared volume. In his prefatory note Professor Thompson says that the book needs no preface since it is all preface. The reviewer would go further and point out that some of the chapters of which the volume is a preface have already been at least partially written but no reference to them is to be found. The vast evidence of the relation of hormones and similar agents to organic growth and form receives scant attention. Nor does the more recent study of the relation between molecular configuration and form and structure receive the hopeful treatment it merits. Moreover, the entire field of the genetics of form is passed by with little comment, and the work of the experimental embryologists and students of regeneration seems to have been overlooked entirely…. No doubt American readers will be surprised at the omission of significant American literature and the absence of names familiar to every modern student of form determination.

In the years following the publication of the second edition this temperate reception gradually became a divide: to many, particularly those with a mathematical disposition, Thompson was a visionary, with a view of biology in which physical and biological law work collectively to produce biological diversity. To others, particularly in the wake of the tremendous progress in cell and molecular biology achieved during the 20th century, Thompson was, due to his apparent opposition to Darwinism, on the wrong side of history and his ideas accordingly began to seem increasingly irrelevant and anachronistic. Indeed an irony of OGF is that it was written as a work of biology, but appealed least to biologists, once their interests shifted towards the genetic and molecular understanding of development. The reasons for its continued popularity arise from Thompson’s status as a multidisciplinary scholar, whose writing has continued through the decades to appeal to a wide audience, including artists, architects, design engineers, anthropologists, and of course mathematicians.

In some ways both assessments are right: Thompson was both anachronistic and visionary, yet, due to the idiosyncrasies of writing style, the modern reader can be forgiven for completely missing the key messages that he tried to convey. To understand these better, let us attempt to tease them out in broad brush.

The primary message of OGF was the need for biologists to adopt a change of mind set, and in particular to embrace the importance of physical principles in biology. Indeed, OGF is addressed to “the zoologist or morphologist [who] has been slow, where the physiologist has long been eager, to invoke the aid of the physical or mathematical sciences” (OGF1, p2). Thompson identifies the availability of numerous theories within the traditional confines of biology, which, “though a little lacking in precision”, have provided
their own routes towards new lines of thinking, and the elaboration and testing of hypotheses, without the need (apparently) for an appeal to the greater precision offered by mathematical and physical theories and methods. In particular, he describes taxonomy (the “art of classification”), as:

> an endless search after the blood relationships of things living and the pedigrees of things dead and gone, (OGF1, pp2-3). ...(Confine to such theories and disciplines stems from)...a reluctance to compare the living with the [inanimate] or to explain by geometry or by mechanics the things which have their part in the mystery of life.

In his view, this inhibited amongst biologists, to their detriment, any move towards applying mathematical and physical techniques and ways of thinking.

Thompson also believed that the search for physical causes and interdependencies encoded in mathematical laws can be fruitfully complemented by another explanatory principle developed by Aristotle – the search for relations between things apparently disconnected, and for “similitude in things to common view unlike” (as quoted by Thompson from Kepler), (OGF1, p6). Many of the examples of analogy Thompson uses in his book, though intriguing in themselves, are of limited value for explaining the development of form in living organisms, even the hard-shelled single-celled foraminifera which he studied in detail. The comparisons between various species of Lagena and forms of Roman pottery, illustrated in (OGF2, pp414-415; Figs 130 and 131 respectively) are of such doubtful value. (In fact, there is no corresponding illustration of Roman pottery in OGF1, just the same illustration of Lagena species, with no mention of Roman pottery at all!) However, as Thompson points out, there is more to analogy than this (OGF1, p6):

> Newton did not shew [*] the cause of the apple falling, but he shewed a similitude … between the apple and the stars ….

Likewise, in OGF2 (p9), Thompson elaborates upon the power of analogy as follows:

> By doing so he [Newton] turned old facts into new knowledge; and was well content if he could bring diverse phenomena under ‘two or three principles of motion’ even though the ‘causes of these Principles were not yet discovered’

In this vein, Thompson argues that traditionally, investigations were more focused on the “differences and fundamental contrasts” between the phenomena exhibited by organic (or animate) as opposed to inorganic (or inanimate) matter, at the expense of seeking “principles or essential similitudes” demonstrating the commonalities relating them. Physicists had long sought unification of the laws of nature as far as non-living systems were concerned, and in so doing approached the “riddles of form” in such contexts as “waves of the sea, the … ripples on the shore, … the outline of the hills, the shape of the clouds”, and many more. Thompson saw these as (OGF1, p7):

* Note Thompson’s archaic spelling “shew”. According to Google n-gram, even back in 1917 this was used by only some 7% of British authors and less than 1% of all authors in English! We have to go back to 1845 to find a time when “shew” is more widely used.
so many problems of morphology, ... solving them by reference to their antecedent phenomena, in the material system of mechanical forces to which they belong, and to which we interpret them as being due.

He urged that things are not otherwise for living things, and that the same (and possibly some other as yet undiscovered), unifying principles should apply in the living as in the non-living worlds. As he famously observed (OGF1, pp7-8):

Cell and tissue, shell and bone, leaf and flower, are so many portions of matter, and it is in obedience to the laws of physics that their particles have been moved, moulded and conformed (and so..) the morphologist is ipso facto a student of physical science.

To illustrate this way of thinking further let us briefly consider a couple of examples. In his first substantive chapter, Chapter II, entitled On Magnitude, (OGF1, pp16-49), Thompson presents observations on the significance of scale and its effects on the growth, functioning and form of organisms that exist at different scales of magnitude. This chapter deals partly with what we would now call allometry – the study of how various properties of an organism scale with size – an area of research that has attracted much interest from both biologists and physicists over the last century. The mathematics of proportionality features strongly throughout this Chapter, a key observation being that surface area to volume ratio declines with increase in spatial dimensions, and this variation places common physical constraints on developing tissues that give rise to the recurrence of similar forms. Thompson gives many examples, e.g. (OGF1, pp32-33), much expanded upon in (OGF2, pp56-57), of cases in which a more or less constant ratio tends to be maintained between mass and surface by means of alterations in form as overall size increases. For instance, whereas the general surface of the body is sufficient for respiratory purposes in smaller species, as organisms increase in size, respiratory area is increased by development of specialised organs such as gills, or the alveoli (air-sacs) within lungs.

Thompson also advocated that the laws of physics should – sometimes most efficiently, and also more intuitively – be expressed, not in terms of governing equations, but in terms of quantities that must be minimised. In fact, this idea is one of the great organising themes of OGF, and one to which Thompson returns again and again - for example in his treatment of honeycombs (OGF1, pp327-334), much elaborated in (OGF2, pp525-544): biological forms derive their structure in large part from the action of physical conservation and minimum principles and similarity in form is, at least partly, due to similarity in underlying conservation principles.

One of the more interesting areas in which this attraction to conservation plays a role is in the famous Chapter XVII On the theory of transformations, or the comparison of related forms..., (OGF1, pp719-777), in which Thompson compares the shapes of related organisms, showing that again and again, the morphologies of related species can be thought of as mathematically distorted versions of each other (by a mathematical process Thompson called the method of coordinates). He argues that similar biological shapes must represent some basic conservation in the physico-chemical developmental process resulting in deformed but still recognisable resemblances in resulting biological patterns. Thompson gave an indication of the principal
forces, and properties of matter, with which we might need to deal in this context, (OGF1, pp12-15). Many of these are familiar and well understood, e.g. cohesion, friction, gravity, pressure from outside the cell, intermolecular forces, and surface tension. When it comes to the (at the time) less well understood ‘forces’ which Thompson characterises as “peculiar to living things”, he uses terms such as chemical, electrical, and thermal influences within the cell, growth as a force arising from chemical and electrical activity, attractions and repulsions within the cell nucleus driving the “caryokinetic figures” of chromosomal movement. At this point Thompson is grasping for language to describe phenomena beyond his reach. Present day researchers would characterise these with greater precision, and they would no longer be seen as peculiar to living things, but explicable in terms of more fundamental physical causes.

Thompson’s main idea – that conservation principles dictate biological form – although attractive, received some legitimate criticism. For instance, the great developmental biologist Conrad Hal Waddington [12], remarked that

(Thompson’s work potentially) opens up a large field for investigation, (but) little has been done to make it into a means of exact analysis. (Medawar has taken some steps in this direction)... by studying the changing shape of the human body from the early foetus to the adult... (but the value of such a procedure is questionable as)... such labour is only justified if it enables one to see certain relations which otherwise would be missed. So far [1956], such evidence of a real usefulness of the method has not been forthcoming”.

This essential criticism – that these are nice ideas but hard to formulate specifically, and do not easily yield biological insight – in part explains why actual use of this idea in the subsequent history of theoretical biology has been very limited.

Thompson stressed at great length the importance of the discipline of mechanics for the development of body forms, and the relationship of those forms to the environments they occupy. However, for physical sciences, the late 19th century was a time of great intellectual ferment, and polymath though he may have been, not all of it came to Thompson’s attention. In particular, he pays scant regard to developments in thermodynamics, with only a cursory mention of the Second Law, and this only in (OGF2, p11). This states that, within a closed system, the measure of disorder (entropy) always increases over time. Clearly this idea sits uncomfortably with the dynamics of living systems, characterised by decreases in disorder during processes of growth and development.

Attempts to resolve this dilemma were very much in the air in the 1940s. For instance, Erwin Schrödinger in his popular paperback What is Life ?[13], speculated upon the relationship between physics and chemistry on the one hand, and the living cell on the other. Schrödinger and (independently) Ilya Prigogine [14], established a theoretical framework allowing life an escape from the second law of thermodynamics. The rule about entropy increase applies only in a closed system. A living system is an open system, continually provided with fuel (e.g. nutrients) whilst discharging waste products into its environment. In these circumstances it is possible for a flow of entropy to counteract the increase in disorder locally,
allowing disorder to decrease locally with time, and the *emergence* of complex biological structures and forms [15].

The importance of Schrödinger and Prigogine to Thompson’s programme lies not so much in the detail, for that is the more domain of the biologist. Rather, it is the realisation that there are overarching physical principles governing developmental biology, and that some features of the developmental process are best understood in terms of general law, in the language of biophysics rather than biochemistry. Thompson emphasised the great extent to which developmental processes, the laws of growth and form, were obliged to obey the laws of classical mechanics, but omitted any mention of the newer science of statistical mechanics [16, 17, 18]. Although Schrödinger’s and Prigogine’s contributions were in the spirit of Thompson, they moved in an alternative direction. The more modern synthesis develops Thompson’s historic programme by including (for example) Prigogine’s *emergent structures* as the natural consequence of the flow of energy and balancing entropy through the complex environment known as the earth’s biosphere.

The narrative expounded above may not be recognisable to a biologist, to whom the dominant mid-20th century figure in the new science of embryology would almost certainly be Joseph Needham (1900-1995). Needham’s two encyclopaedic contributions – his three volume *Chemical Embryology* (1931)[19] and his follow-up 757-page *Biochemistry and Morphogenesis* (BM) (1942) – sit astride the field of developmental biology, transforming the developmental process from *deus ex machina* to complex biochemistry amenable to the experimental method. By way of example, it was Needham, among others, who showed that Hans Spemann’s (1924) embryological “organiser centres” [20] could not be interpreted within a vitalist framework, but by contrast had a chemical origin. Cambridge University Press published editions by both Needham and Thompson in 1942, but we venture to guess that to the practical biologist, it was Needham’s careful exposition of experimental method, rather than Thompson’s prophetic vision which was more useful. Even if, philosophically, they were singing from similar hymn sheets.

It is of more than passing interest that Thompson and Needham are two of the few scholars who have successfully straddled the humanities-science divide (so famously deprecated later by C.P. Snow in his essay about the “Two Cultures” [21]). Needham, like Thompson, faced the problem of ontogeny as a philosophical problem, in his case to be addressed using the chemical tools with which he was familiar. He was later to abandon science almost completely. Notwithstanding his enormous reputation as a biochemist, he is even better known for his authoritative set of volumes on the History of Chinese Science [22]. As a result, he achieved the distinction of being a fellow of both the British Academy and the Royal Society, rare at least partly because it was a reward for merit in distinct fields. But notably absent from Needham’s work was much mention of mathematics. But somehow the spirit of his work was nevertheless calling out to the profession, as witnessed by these remarks by the Chicago mathematician Alston Scott Householder [23] in his review in the *Bulletin of Mathematical Biophysics*:

……even a casual reading of the book one finds many places where quantitative theoretical formulations seem called for…. such terms as "competence", "determination", "potency", and the like, are so clearly in need of quantitative, rather than qualitative, treatment that a feeling of impatience is
hard to suppress……. It is not necessary to comment on the important role that must be played in the
development of the subject by such a comprehensive outline by an outstanding authority in this field.
Mathematical biophysicists in particular, will find it invaluable when they do undertake any work on
problems of development.

Subsequent 20th century history of the subject focusses on biochemistry, and its offspring molecular
biology. The unfolding but still unfinished story of the role of DNA in the developmental process first
revealed the importance, and then the function of DNA in genetic transmission, before Watson and Crick
[24] finally disentangled its structure in 1953 [25]. Progress has continued, in leaps and bounds, as
successively (to cut a very long story short) the role of RNA and of regulatory genes, the existence of
regulatory gene networks, and structure of the human genome itself were discovered.

But mathematicians and chemists often talk a different spiritual language. What constitutes
intellectual organisation for the one, is for the other mere verbiage, or worse deliberate obfuscation. For some,
equations and mathematical concepts are great simplifiers, while for others they rather hide the obvious in a
mass of incomprehensible squiggles. The evolutionary biologist Stephen Jay Gould, a great populariser,
almost a poet, but neither mathematician nor chemist, averred that molecular biology alone could not replace
the “concept of form and spatial structure”, and it was the latter which was Thompson’s main concern.

In similar vein, it was Alan Turing, the pioneering mathematician and computer scientist, who asked
himself the question, how, in principle, might it be that non-uniform chemical states might emerge from an
initially formless aggregate of cells [26]. Here, rather than in the apparently endless chemical detail from the
biochemists and molecular biologists, sprang the first green shoots of Thompson’s intellectual vision. There
are six references in Turing’s paper: a single one to a journal paper, that of Michaelis and Menten [27] (albeit
a classic dating from 1913!), three to biology books, and one to a physics book. The last reference, fifth out
of six in his bibliographical list (although apparently unmentioned, so why it is there is a mystery) is to OGF2.
Turing’s final paragraph is characteristically modest:

……the biological examples….in the present paper are very limited. …… biological
phenomena are usually very complicated……..one could hardly expect to find that many
observed biological phenomena would be covered. It is thought, however, that the
imaginary biological systems which have been treated, and the principles which have been
discussed, should be of some help in interpreting real biological forms.

Of interest in the intellectual history of the 20th century here is not only the “generalisation of
simplification” from the physical to the biological sciences, not only the understanding of a key biological
process giving rise to the structure of the biological organism [28], not even the demonstration of an
intellectual route from Thompson and OGF to modern theories of differentiation, nor yet the application of
mathematics to biology (not yet widespread, but beginning to diffuse from major universities already from the
1920s and 1930s). Turing formulated some non-linear differential equations, which even he needed to solve
on the computer. Luckily, well, it was more good management than good luck, of course, as he was the major
driver, he was working in one of the few universities in the world possessing one such.
Let us fast-forward to the present day. Our knowledge of the minutiae of the biology of the organism is incomparably greater than in 1917. The vitalists, still influential in 1917, now possess the same status as believers in Asgard, Olympia or a flat Earth. Computers, unknown in 1917 except in the Babbage’s somewhat faded theoretical speculations, have increased in power by a factor of $10^{15}$ since the time of Turing, rendering previously savage and mysterious sets of simultaneous differential equations soluble in the blink of an eye. Physicists and chemists have advanced from the van der Waals theory of the phases of simple materials (why is there a liquid and a gas phase and what is the difference?) to complex theories of fluids of interacting particles of different shapes and sizes. Within the lifetime of the present writers, the mysterious cytoplasm has degenerated into merely another non-equilibrium complex fluid. As we have seen above, an understanding of the physics of life becomes an application of statistical mechanics of out-of-equilibrium systems. Connections are found between protein function, protein shape, and protein chemistry and forces experienced by the protein molecules. Meanwhile, astrobiologists muse as to the requirements of life on planets very different from our own, and speculate as to whether DNA or the genetic code is unique.

Mathematics too has acquired new strings to its bow. The bifurcation theory of dynamical systems (so pithily summarised simply as “catastrophe theory”) enables simple organising principles to emerge from initially complex systems. Symmetry, and sometimes either the lack of it or changes in it, have attracted much mathematical interest, and the relationship between such theories and the different symmetries in different animal or plant phyla have not gone unnoticed. Defects in fluid fields in living cells, described using topological classifications which did not exist in 1917, are revealed as engines which conduct energy from micromotors to larger scales. The deformations noted by Thompson apparently transforming one species to another are revealed as the results of waves of cellular differentiation occurring at different times and in different orders in different organisms. Interacting processes, whether during development or simply while occurring on a day-to-day basis, turn out to be describable in terms of graphs, whose properties can be studied by mathematicians and physicists independently of the biochemical details which inspired the graph models in the first place. Advances in computation and statistical analysis of data enable rapid and reliable analyses of phylogenetic relationships even where convergent evolution of phenotypic features muddied the waters. And Claude Shannon’s theories [29] introduced ideas of entropy into theories about information, an entropy which, it turns out, can at the end of the day be exchanged for Clausius’s more well-established thermodynamic entropy.

And so on. To summarise, despite its many shortcomings, OGF remains one of the most important books in 20th century science, articulating a broad, and surprisingly modern, vision of science, in which the disciplines work in harmony to understand the natural world. This, rather than the specific details of OGF, is Thompson’s enduring legacy. His cult status is no doubt partly to do with the grand sweep of his ideas, ranging, as they do, over the whole range of the sciences and the arts. But the grand sweep is, paradoxically, also a major drawback, for detailed scientific argument is renounced on the basis of an epiphanic faith in the manner of scientific progression. In the view of the present authors, part of Thompson’s difficulty, perhaps
like that of Charles Babbage, was that he was premature. Babbage in the 19th century could not build a successful analytical engine because to make it work on the scale required; he really required electricity and the whole panoply of modern electronic circuits [30]. Likewise Thompson in the early 20th century could not quantify biology, because neither enough biology, nor enough of the basic underlying physics and chemistry were yet understood, and in any case, even had they been, the mathematical tools available at the time were inadequate. Now it is otherwise. Now, the so-called “Third Revolution: the convergence of the life sciences, physical sciences, and engineering” [25] is in full swing. Now we have the tools, we think (but who can be sure?) but the job is not yet done. It is, so to speak, the end of the “preface”. Quite how long it will take for the rest of the book to be written, and by whom, that is a question for the century to come.
References


8. For an influential contemporary book, see e.g. W. Bateson, *Mendel’s Principles of Heredity* Cambridge University Press, 1913). Bateson included translations from the German of some of Mendel’s original papers in this volume.


20. For a discussion of the relevant history of embryology from a biological viewpoint, see e.g. V. Hamburger, The Heritage of Experimental Embryology: Hans Spemann and the Organizer. (Oxford University Press, 1988).


28. For further discussion of the influence of Turing on modern work in biological pattern formation, see e.g. P.K. Maini. The Impact of Turing’s work on Pattern Formation in Biology. Mathematics Today 40, 140-141, (2004);

H. Meinhardt, Turing’s Theory of Morphogenesis of 1952 and the Subsequent Discovery of the Crucial Role of Local Self-enhancement and Long-range Inhibition. Interface Focus 2, 407-416 (2012);


30. For a background to Babbage and computing, see e.g. D.S. Halacy. Charles Babbage, Father of the Computer. (Crowell-Collier Press, 1970).