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*On Growth and Form*:   
Context and Purpose

Florian Jabbour1 and Guilhem Mansion2

1 National Museum of Natural History, Paris, France

2 Freelance biologist, Zurich, Switzerland

Published in 1917, and then in highly-expanded version in 1942, *On Growth and Form* is a book written by Scottish zoologist D’Arcy Wenworth Thompson, who was a professor at the University of St Andrews, and holds an almost legendary place in the scientific literature, and even beyond. As in all legends, it has inspired people in every era, as shown by the various commentators who have made it out to be the work of a mathematician, a lone heretic, or an amateur against the modern aspects of biology. But what place did D’Arcy Thompson really hold in the scientific community in which his long life (1860–1948) took place? In order to judge it, as well as evaluate its influence until the 21st Century, it is necessary to refer to the sources and go beyond the simple overview of this popular book. One will be astonished when lured into a historical examination of the debates that have marked the life sciences at least since the beginning of the 19th Century, and especially since the publication of Charles Darwin’s first book in 1859. It is from the elements of Thompson’s life, his professional career, and his working relationships that it is possible to understand this intellectual plunge, the concepts discussed, and to trace the maturation of his ideas in agreement or disagreement with the protagonists of the adventure – that of the process of consolidating a theory of evolution. He was 57 years old when he published this work in 1917. He already had a long career behind him: 32 years as Professor of Biology at the University College of Dundee, where he created a museum of zoology, following which he was appointed Chair of Zoology at the University of St Andrews. He is known for his translation of Aristotle’s *History of Animals* in 1910, but equally for his translation of Herman Müller’s *Die Beruchtung der Blumen durch Insecten* in 1883, which Charles Darwin wrote the preface to in a work that founded the concept of co-evolution. He was also an expert in marine biology and an advocate for endangered species, particularly the marine otter fur hunt in the Bering Strait. In his museum, he had collected a skeleton of the Steller’s sea cow, a giant sirenian that had recently disappeared from those areas. In Dundee, he was an administrator of the hospital and founded an association for the housing of poor families. Lastly, he had a passion for mathematics, which he practiced as an amateur.

Peter Medawar has devoted several pages to *On* *Growth and Form* (1984). He underlines its originality, both in style and language (which he describes as: “I think that *Growth and Form* is beyond comparison the finest work of literature in all the annals of science that have been recorded in the English tongue”), and in ideas, which he finds timeless. And yet, this landmark must be placed on the movement of ideas that agitated scientific and philosophical circles between 1880 and 1930, regarding the theory of evolution. Espinoso (2014) consulted D’Arcy Thompson’s correspondence, which allowed him to appreciate the importance of his relationships with some of the key players in the biology community of his time. Thompson belonged to the generation of British students who were immersed in the debates that followed the first steps of Darwinism. Comparative anatomy and embryology dominated then, and were brought to the heart of the debates on phylogeny by Thomas Henry Huxley, Ernst Haeckel, Karl Gegenbaur and Oscar Hertwig (Gasc 1996a). It was also the period of discovery of the marine world and new models of study in newly created research stations. The mechanism of fertilization is depicted in algae, the first cellular phases of embryonic development in sea urchins. His translation of Müller’s book on pollination in 1883 shows his involvement in the ongoing debates from his youth, and he participated in the development of marine biology through numerous publications on organisms whose diversity was being discovered. German universities and laboratories have been an international magnet for English students. Anton Dohrn (1840–1909), a graduate of the University of Jena where he was a pupil of Haeckel, founded the Stazione zoologica di Napoli (Zoological Station of Naples) in 1872. This experimental research station is part of a network project (inspired by the railway model!) that is international. It has played an essential role in understanding embryonic development, using marine organisms as models. The “Vivarium” in Vienna (Biologische Versuchsanstall) was founded in 1902 by Hans Leo Przibram (1874–1944). It is an international laboratory which allowed work in “experimental zoology”, where biological and physical-chemical approaches were combined, following on from the work of Berthold Hatschek (1854–1941). Best known for his work on the embryology of the Amphioxus and his hypotheses on the origin of bilaterians, Hatschek was interested in the physical-chemical properties of “colloids”. He obtained *mimics* of organic forms, jellyfish and polyps, from mixtures of substances. Thompson’s correspondence preserved at the University of St Andrews reveals the close and lasting relationship between him, Hatschek and Przibram. Most of the experimental examples cited in *On Growth and Form* are the result of these exchanges, because he was not an experimentalist. Müller (2017) cites this situation described by the mathematician and historian Marjorie Senechal:

Where D’Arcy Thompson saw analogues, the Przibram brothers did experiments. Where he found elegance and simplicity, they found chaos and complexity. Where they glimpsed biological laws, he suspected leaps of imagination. But [he] and the Przibram were allies in the nascent international campaign to infuse biology with physics and chemistry.

Indeed, the Vienna Vivarium was the international crucible of a trend of experimental biology, directly derived from the comparative anatomy and embryology of the 19th Century, which, fertilized by evolutionary ideas, would focus on the conditions in which the early construction of organisms took place. This trend also includes the influence of Wilhelm Roux (1850–1924), again a pupil of Haeckel, whose *Entwickelungsmechanik* (“mechanics of development”) opened up the confluence of heredity, environmental factors and functional activity. This is obviously a field that does not fit in with the dominant developments in biology following Weismann, de Vries and Morgan. Indeed, at the end of the 19th Century, morphologists were mainly concerned with phylogeny, the relationships of filiation between large groups of multicellular organisms. Haeckel’s influence was noticeable, even if his “fundamental biogenetic law” of recapitulation, which nested phylogenesis within ontogenesis, staggered in the face of the number of exceptions discovered by the work of embryologists. Under the banner of Darwinism and with great talent, Haeckel defended a syncretic doctrine in which a trace of pantheism from the *Naturphilosophie* of the German romantics and a reference to Lamarck coexisted. However, in 1885, August Weismann (1834–1914) closed the door to the notion of a heredity of traits acquired in the course of individual life. He laid down the rule that organisms are composed of two independent cellular compartments. On the one side, the “germ plasma” consisting of the gametes that ensure generational transmission, resulting from a particular mode of division described by Hertwig, and on the other side, the somatic cells that ensure daily functioning and disappear when they die. This is a real conceptual revolution in the life sciences (Buss 1987). Until then, “soft” heredity, associated with Lamarck, as well as the “use and no-use” evolutionary rule, was accepted by all, including Darwin, as a mechanism for the transmission of traits and a source of transformation. Shortly afterwards, Hugo de Vries (1848–1935) rediscovered Mendel’s laws, which demonstrate the independence of “factors” in hereditary transmission, and revealed the frequency of discontinuous variations, which he called “mutations”. It was then that with the experimental program of the Thomas Hunt Morgan School (1866–1945), adopting Drosophila as a model, a new discipline was born: genetics. At first, it focused on the mechanisms of hereditary transmission through the interplay of corpuscles, the material support of Mendel’s “factors” that Johannsen called “genes” in 1909 and which are located in chromosomes.

Most morphologists will refuse to fall by the wayside, especially embryologists, who chart a distinct course, leaving phylogenetic considerations to paleontologists and concentrating on experimental analysis of the sequence of events during embryogenesis. In short, coming back to the original mind of Karl von Baer. Biology is no longer a unified science and, while the theory of evolution is part of the conceptual landscape, the mechanisms proposed by Darwin are sidelined, especially the role of chance in variation and the intervention of natural selection. This is “the eclipse of Darwinism” (Bowler 1983). In this context, D’Arcy Thompson takes a distant, even distrustful attitude towards what he calls “modern biologists”, and pursues an original program.

4.1. D’Arcy Thompson’s program

As original as it is, this program is nevertheless part of a school of thought that wanted to refute the division of sciences exposed by Immanuel Kant. Indeed, according to Kant, on the one hand there are the “Newtonian” sciences, where universal laws based on the quantification of phenomena apply, and on the other hand, there are sciences such as those dealing with the living world, where finality dominates and whose complexity would prevent the application of quantification procedures. Some of Kant’s German pupils were guided, following Schelling, to promote a “Naturphilosophy” which sought laws specific to living beings, that were also universal and even cosmic. This was the breeding ground for a vitalist movement and attempts to introduce a mathematical approach referring to Pythagoras, such as among the anatomists Oken and Carus, led to speculations bordering on the mystical. At the same time, and also influenced by Kant, Georges Cuvier laid down the principles of a correlation between the organs involved in vital functions. Thus, in his search for Kantian criteria, he did not hesitate to compare the relationships he observed in mammals to a mathematical equation, such as those between diet, the shape of the mandibular condyle, the type of teeth, the composition of the digestive tract and the shape of the tip of the legs (1812). Founding comparative biology, he states his ambition: “whoever would rationally possess the laws of organic economics could remake the whole animal.” It is also with ambition that D’Arcy Thompson begins his work with a long introduction, a form of epistemological reflection that allows him to situate this book in the history of life sciences and its relationship with philosophy. He summarizes his program in these words:

We want to see how, in some cases at least, the forms of living things, and of the parts of living things, can be explained by physical considerations, and to realize that in general no organic forms exist save such as are in conformity with physical and mathematical laws. And while growth is a somewhat vague word for a complex matter, which may depend on various things, from simple imbibition of water to the complicated results of the chemistry of nutrition, it deserves to be studied in relation to form: whether it proceed by simple increase of size without obvious alteration of form, or whether it so proceed as to bring about a gradual change of form and the slow development of a more or less complicated structure.

Everything is said in this passage, with the inimitable literary style of this author. He then develops this program at the various levels of integration of the organization, considering the dominant forces for each of them. At the cellular level, it is the surface tension, with the effects of surface revolution and the conditions of stability, which leads to a limited number of forms. The association of tissue cells and the conditions of stability of the forces present obey the same constraints of surface energy, and the state of equilibrium leads to the hexagonal shapes so generally widespread. Thompson cites a long passage by Buffon in this connection which, in his *Natural History*, already mechanically justified the generality of this symmetry that makes it possible to divide a space by limiting the contact surfaces. At the level of organs, he examines the case of the blood vessel connection system, based on the hypothesis of a minimum energy cost for the cardiac muscle in the face of the need to deliver oxygen to the whole organism.

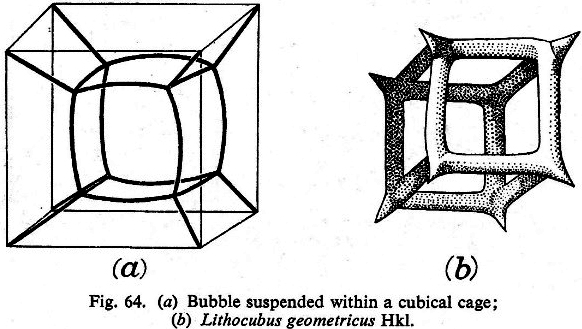
In particular, he is interested in the relationships between the cross-sectional areas at successive levels of the vessel connections. As the resistant friction increases as the diameter decreases, it is expected that the sum of the capillary areas will exceed the area of the original trunks, if our reasoning is it is to limit cardiac expenditure. It should be noted that, on this subject, D’Arcy approaches the concept of symmorphosis, later developed in physiology by Weibel *et al*. (Gasc 1999), in search of an optimization of structural-functional relations; however, these authors have a Darwinian perspective of selective advantage, which he rejects.

Support structures (skeletons of single-cells, shells and dynamic vertebrate architectures) are widely developed. In this field, Thompson is confronted with the complex problem of the chemistry of associations between “colloids” and crystalline forms of calcium salts, carbonates and silicates. In his time, research in biomineralization was only at the stage of describing the structures, and Haeckel‘s theories on the genesis of these formations and the position of mineral spicules between the cells of sponges by an evolutionary phenomenon of selection seem, to him, to be refuted insofar as similar forms are found in distant beings in the classification, and therefore, according to Haeckel, without a close ascendant. The finesse of his argumentation can be seen in his position on the very ground of the theory which he declares not to be adhering to, revealing the trap of what are today called homoplasias, and questioning the a priori phylogenetic value of any trait. He is clearly convinced that physical forces are more important than phylogenesis in determining the form of organisms. Thus, by analyzing the spiral forms of mollusks, he indicates that the simple speed of the generating curve during growth determines the difference in shell forms. However, it is with regard to the variations in the form of radiolarians, which can be followed over millions of years, that he would be more explicit in his rejection of a systematic application of the concept of evolution over time:

… the question stares us in the face whether this be an “evolution” which we have any right to correlate with historic *time*. The mathematician can trace one conic section into another, and “evolve” for example, through innumerable graded ellipses, the circle from the straight line; which tracing of continuous steps is a true “evolution”, though time has no part therein.

This can be expressed using the following formula:





a) b)

Figure 4.1. Experimental creation of analogous forms in On Growth and Form.  
 a) Bubble enclosed in a cubic cage; b) skeleton of a radiolarian

However, Thompson thus denounced the confusion made by many evolutionists of his time between morphological series and evolutionary series, and he questioned the role of a natural selection of the “most capable” forms:

That things not only alter but improve is an article of faith, and the boldest of evolutionary conceptions. How far it be true were very hard to say; but I for one imagine that a pterodactyl flew no less well than does an albatross, and that Old Red Sandstone fishes swam as well and easily as the fishes of our own seas.

With the chapter entitled “On Form and Mechanical Efficiency”, he analyzes examples of the relationship between form and function; in other words, he addresses the delicate issue of adaptation. Referring to the techniques of the engineer and the experience of builders, he is then in line with biomechanics, from Borelli’s *De Motu Animalium* (1685), and his contemporaries, with the work of Georg Hermann von Meyer (1815–1892) and Julius Wolff (1836–1902), who interpreted the orientation of the trabeculae of bone tissue in human beings in terms of the mechanical strains in relation to the erected station. However, and contrary to Wolff, who placed his famous “law” of minimum bone substance for optimum efficiency in the Darwinian perspective of selective advantage, he rejected any genetic influence in processes where form seems to be congruent with function:

In the biological aspect of the case, we must always remember that our bone is not only a living, but a highly plastic structure; the little trabeculae are constantly being formed and deformed, demolished and formed anew. Here, for once, it is safe to say that “heredity” need not and cannot be invoked to account for the configuration and arrangement of the trabeculae: for we can see them at any time of life in the making, under the direct action and control of the forces to which the system is exposed.

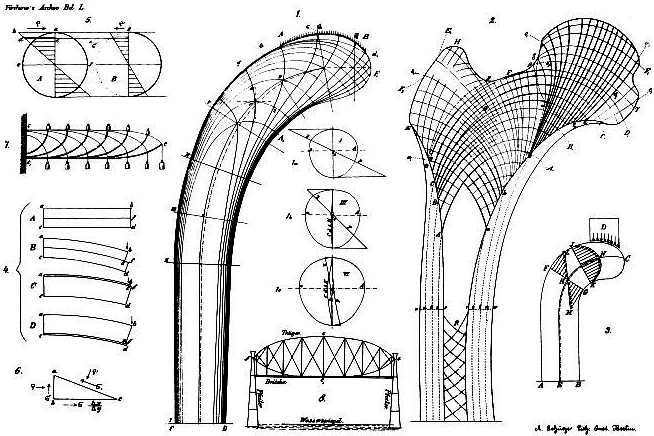


Figure 4.2. Illustration of “Julius Wolff’s Law” (1892),   
always in the spotlight in orthopedic surgery

Note.– According to Thompson, therefore, the adequacy between form and function results from an adaptation of the organism to immediate physical conditions and not from an adaptation in the evolutionary sense. As for the skeletal framework as a whole, comparison with buildings, in particular with the various categories of bridges, enables him to highlight the need to consider it above all as an assembly of bony parts, tendons and muscles mobilized in actions. But, above all, he insists on the difficulty of moving from a static vision, that of buildings, to an understanding of the dynamic conditions in which this osteomuscular system intervenes in movement. Why did he overlook the French school of biological physics (1901), led by the engineer Gariel, the veterinarian Chauveau, the physicist d’Arsonval and the physiologist Marey? It can also be noted that the program he presents leads to functional morphology, through the steps of Hans Böker (1935–1937), James Gray (1944) and McNeil Alexander (1968). This injunction to consider the organism as a whole while immersed in a system of forces led him to, on the one hand, adopt a holistic perspective, and on the other, to call upon a Lamarckian mechanism. Critical of the excesses of the phylogeneticists of his time, mainly paleontologists such as Henry Fairfield Osborn (1857–1935), who promoted orthogenesis and rightly denounced syllogisms and the use of isolated traits as phylogenetic markers, Thompson remained skeptical of the theory of evolution. This reserve would be shared by many biomechanicians (Gasc 2006). Nevertheless, the Russian school, little known because it was a victim of the obligation not to publish outside the USSR during the Stalinist period, developed an “evolutionary morphology”, in line with Alexei Nicolaevitch Severtsov’s thought (1866–1936), through a series of comparative studies of adaptations of the locomotor and manducatory apparatus, where the rules of rational mechanics are applied (Yudin 1957; Dzerzhinsky 1972; Gambaryan 1960). The 1974 pirated translation from Russian into English of *How Mammals Run: Anatomical Adaptations* by Peter Pavel Gambaryan, the French-Russian collaboration on bird beaks (Korzun *et al.* 2004), and the recent work on the origin of flight in mammals (Panyutina *et al*. 2015) demonstrate the effectiveness of biomechanics in the framework of the Darwinian theory of evolution.

4.2. Application of mathematics to morphometry

The best-recognized contribution of *On Growth and Form* is contained in the chapter entitled “On the Theory of Transformation, or the Comparison of Related Forms”. It is indeed in these pages that D’Arcy Thompson conducts his reflections on the use of mathematics in the definition, description and thus comparison of living forms. His reasoning is inspired by the adage attributed to Galileo Galilei: “the book of Nature is written in the characters of Geometry”, but also by the definition of form enunciated by Aristotle, which he had translated in his youth and for whom form takes precedence over matter. The starting point is on the field of comparison. In the search for recognition and classification, the difference between two forms is expressed in terms of proportion, of relative size. The Cartesian coordinate method, which characterizes the form of a mathematical curve, and therefore its equation, is then imposed. On the condition that the comparison is made between related beings, in other words, those that are homogeneous in their composition, by using invariant landmarks, it not only becomes possible to replace a description by a quantified definition, but to also highlight the sites of deformation, to put oneself on the path of the cause of transformations, thus returning to Goethe’s initial definition of morphology, in search of “metamorphoses”. The figures that Thompson produced, which have become so classic, reminiscent of the anamorphoses of painters, are applied to various groups of present-day and fossil beings, and even to the various forms of leaves and their arrangement along the stem (phyllotaxis). Taking the example of the pelvis in the lineage of birds, it calculates intermediate configurations and reveals the remarkable stability of the general form. It also shows the ability of this method to remove a fossil from a presumed continuous lineage over time when anisotropy occurs.

Table 4.1 demonstrates this point.

|  |  |  |  |
| --- | --- | --- | --- |
| **Text** | **E** | **F** | **G** |
| **A** | 1234 | 5678 | 9101112 |
| **B** | 13141516 | 18192021 | 2223.2425 |
| **C** | 26272829 | 3031.323234 | 35363738 |
| **D** | 39404142 | 43444546 | 47484950 |

Table 4.1. Demonstration of text

Of course, for Thompson, this method essentially shows the direction of the forces that are responsible for changes in form; in other words, it indicates the relationship with function. However, he is aware that his approach is limited to an outline, to a projection on a plane, without integration of the third dimension. To present the method, he chooses fish, because their silhouette alone is a source of information for their recognition and the study of their growth.

It is precisely this zoological example that was at the origin of a veritable explosion of work in the new field of “geometric morphometry”, long after his death (Bookstein *et al*. 1985). In 1988, at the congress of the American Society of Ichthyology in Ann Arbor, University of Michigan, a workshop was held that revealed the resources of computer applications in form analysis. The presence of many zoologists and paleontologists from around the world at this workshop led to the rapid spread and further development of these methods, of which D’Arcy Thompson was the first designer (Bookstein 1982). Researchers now have the tools they lacked: taking three-dimensional coordinates, modeling the image and immediately processing a very large amount of data, thus making statistical control possible (Rohlf and Marcus 1993). The field of applications of geometric morphometry is very broad, from the study of fossils to expression recognition (Baylac *et al*. 2003; Gielis 2003; Mardia *et al.* 2018). In a critical review that is unfortunately limited to American literature, Cooke and Terhune (2015) rightly point out that it is a complementary technique, in particular to studies of functional morphology.

However, it would be wrong to limit D’Arcy Thompson to this illusory pioneer role of a method and to limit oneself to quoting his work in the last chapter! Just as Darwin’s thought is often caricatured because it is quoted without having been read, *On Growth and Form* deserves special attention. In its profusion and despite the inevitable obsolete passages, it is a major and coherent work. In particular, it contains a profound reflection on scientific research involving the unity of the sciences, which was against the trend in the early years of the 20th Century, a time of babelization resulting from the specialization of disciplines. On the other hand, a century later, it appears to be on the right track. His positions on the theory of evolution and early genetics must be seen in the light of a fiercely independent spirit that was irritated by the dogmatic positions and assertions expressed in these fields by many of his contemporaries. On the other hand, it is surprising that he did not grasp the scope of the application of mathematics to the study of evolutionary processes, a movement which developed from the 1920s onwards in the study of hereditary transmission and natural selection in the extension of genetics to populations, since he did not mention it in the revised 1942 edition. Similarly, the advances in biochemistry that would be decisive in evolutionary biology did not attract his attention. In fact, his mind was entirely turned towards the geometrization of patterns and he deliberately limited the study of processes to the action of physical forces that were external to the work in the elaboration of forms.

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