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# Emergence and Function of Complex Form in Self-Assembly and Biological Cells

**Stephen T. Hyde**

Department of Applied Maths, Research School  
of Physical Sciences and Engineering, The Australian  
National University, Canberra 2601, ACT, Australia

**Gerd E. Schröder-Turk**

School of Engineering and Information Technology,  
Murdoch University, Perth 6500, WA, Australia

**Myfanwy E. Evans**

Technische Universität Berlin, Department für Mathematik,  
Strasse des 17. Juni 143, 10623 Berlin, Germany

**Bodo D. Wilts**

Adolphe Merkle Institute, University of Fribourg,  
Chemin des Verdiers 4, CH-1700 Fribourg, Switzerland

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This year, 2017, marks the centenary of the first publication of 'On Growth and Form', by the extraordinary Scottish classicist, biologist and part-time mathematician, D'Arcy Wentworth Thompson [1]. Its 800-odd pages (expanded to more than 1100 pages in later editions, and now cruelly abridged) have in parts dated, in others not, but it continues to offer an important thesis: geometry, physics and engineering can and must inform biology. Biologists continue to demur on Thompson's importance. After all, he remained a staunch anti-Darwinist, and his book can be interpreted as an alternative to Darwin's theory of design. He is therefore viewed by the

biological orthodoxy as an outsider. Nevertheless, some of his greatest admirers were among the very best contributors to the biological sciences: for example, Peter Medawar [2] and Stephen Jay Gould [3] both championed his work, leavened with their own modifications.

Today, the physical sciences extend much farther into the domain of biology, driven in parts by the explosion of computational techniques and computational power to numerically tackle systems with the complexity typical of biology. Much of that effort is focused on genetics and evolutionary biology. On the conceptual level and related to structure formation, geometric and physical principles continue to be invoked to further our understanding of the formation of biological or self-assembled structures, from the concept of bending rigidities to mechanisms of non-linear pattern formation in (for example) reaction-diffusion systems. Surely Thompson would be gratified to note the increasing relevance of non-linear growth models, that, thanks to the advent of computers, generate patterns with far richer morphologically than the soap bubbles he played with. Examples are many, but include models of the folded brain [4] or the form of the gut [5], as well as the intricate minimal or constant mean surface forms with bicontinuous morphology found in synthetic self-assembly and biology (see the contributions in this collection about bicontinuous structures in butterfly nanostructures [6], in inner-cellular membranes of amoeba [7], and synthetic self-assembled phases [8]).

To our knowledge, no counterpart with the stature and universality of Thompson has emerged to champion the converse hypothesis: that biology itself has much to inform the physical and mathematical sciences. We need one. One of us (STH) recalls a letter sent to his then supervisor, Sten Anderson, in Lund in the early 1980's from the greatest 20th century geometer, William Thurston. Thurston, answering a query we had about the hyperbolic plane, urged us to 'study the form of leaves' (to paraphrase). Evidently, the great Thurston implicitly appreciated the importance of the natural world in informing how we think about mathematical forms. Today, the study of curvature and structure in materials, both living and dead, is active and resulting in profound insights into materials science, physical chemistry and biology. These insights are beginning to inform studies in mathematical and theoretical disciplines, in the way that they already have influenced architecture and design [9, 10].

These papers collected here comprise a written record of a rain-soaked meeting held in 2016 at an otherwise glorious location, on the south-west

coast of Australia, in Yallingup, see Figures 1 and 2. It is a healthy testament to the importance of Thompson's pioneering insights that the spirit of 'On Growth and Form' pervaded the meeting, though mostly unconsciously. The aim of the meeting, that we hope is reflected in this volume, was also to explore the interstitial space between the physical and natural sciences, between living and dead form. Today, there is a growing awareness that there is an important zone that straddles both domains. So, for example, the similarities and differences between classical faceted crystalline deposits of minerals, and nanostructured biominerals, converge in the nanosciences [11]. As Gould has argued, Thompson was a confirmed Platonist, wedded to the notion of optimal forms in nature as well as physics. This question of optimal form, while often overlooked, remains important, in the context of both ordered and disordered geometries. Plato lives! Optimal bicontinuous and tricontinuous forms are indeed relevant to membranes both *in vivo* and *in vitro* [12, 13] and pure geometry is an elegant route to understanding helical fibre arrangements [14, 15].

A second strand of Thompson's thesis is equally important and remains relevant: understanding of complex spatial forms in nature relies on the details of the physical forces at play, rather than resorting to evolutionary principles alone. While shape and form adapt through evolution, this process is mediated by the physical forces and principles that actually shape the material. Again, this collection offers some insights, both relating to the very same forces that Thompson was considering (surface tension, [16]), as well as more complex interfacial forces [17] and interactions [18], as well as entropic principles [19] and non-equilibrium effects in pattern formation [20]. In our view, science must ultimately reconcile the geometry and forces approaches, that remain largely divorced from each other. Thompson's brilliant idea that load-bearing structures in biology reflect their stresses, and are a "diagram of forces" still has no analogue at the sub-cellular (and down to macromolecular and atomic scales), where we now know that the bulk of biological functioning goes on. Contributions in this collection address the complex issues of multiple length scales in composites, from the shapes of microstructured emulsion droplets [21] to the intriguing optical features and structural colour in nature, probed by microscopic imaging of insect and butterfly nanostructures [22, 6] and circular-polarisation effects therein [23].

The breadth of studies reported in this collection will, we hope, encourage those younger scientists, looking to find their own research niches, to explore this interstitial zone that draws on engineering and biomechanics, geometry

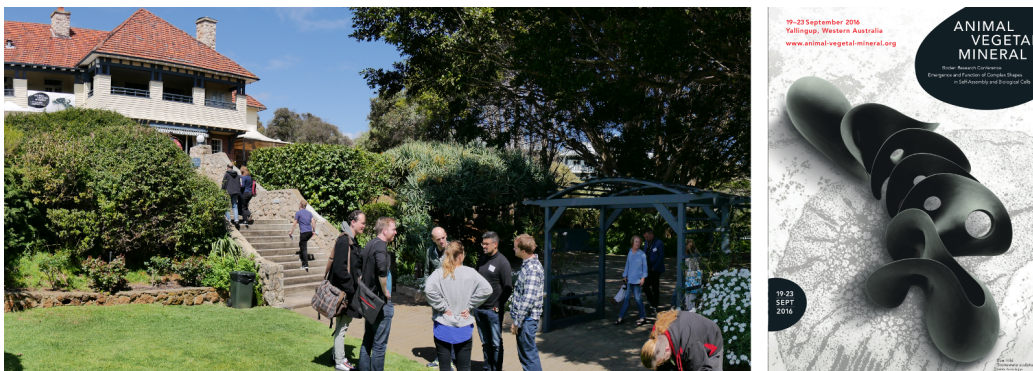


Figure 1: Conference poster for and venue of the 2016 Boden Research Conference 'Animal, Vegetal, Mineral', held at Caves House Hotel in Yallingup, Western Australia, from 19-23 September 2016. The design of the conference announcement poster was based on a sculpture by Eva Hild. (Photography of venue by Benjamin Apeleo Zubiri)

and topology, surface forces, etc.

There is no doubt that this is an area that demands more careful research. Today, both popular and science media report weekly findings of planets beyond our own solar system, usually accompanied by almost *de rigueur* claims that life will be found elsewhere, and soonish. But what constitutes and characterises *in vivo* forms compared to abiotic matter? We do not yet know. The dead-living divide is surely spanned by a spectrum of intermediate forms and materials, whose features retain aspect of both worlds. The work published here, and the discussions in Yallingup, will, we hope, assist to inform the broader questions of science, from the existence of extraterrestrial life to new ways of thinking about structure and function, in biology, engineering, physics, materials science and mathematics, as well as in architecture and design. These are big questions lying behind the daily fruits of science, often shied away from in today's competitive climate.

D'Arcy Thompson was reputed to have been offered a choice of three professorships at Dundee: mathematics, classics or zoology. (He chose the last.) Contemporary science is very different, and the broader tapestry is more likely to be woven by many specialists. This volume will, we hope, afford a modest contribution to encouraging genuine profound discourse and engagement across the discipline boundaries of the 'dead' and the life sciences, in the spirit of D'Arcy Thompson's philosophy.



Figure 2: Group photos of the attendees of the 2016 Boden Research Conference 'Animal, Vegetal, Mineral', taken during a rare break in otherwise incessant rain. The conference was attended by 76 scientists, including 50 international participants, with 11 keynote lectures, 10 invited talks, 27 contributed talks and 23 poster presentations. (Photography of participants by Robert Corkery).

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