INTERDISCIPLINARY SCIENCE REVIEWS, Vol. 38 No. 1, March 2013, 12–34

D'Arcy Thompson's Legacy in Contemporary Studies of Patterns and Morphology

Stephen T. Hyde
Australian National University, Australia

D'Arcy Thompson's views on the forms of biomaterials are assessed in the light of current thinking on biomorphology in selected areas of biology. It is clear that his guiding concepts — that biological materials are structured in response to physical forces, and that the biological and abiotic realms share many common features — remain valid. Advances in the physical and biological sciences are discussed, from quantum mechanics and molecular biology to liquid crystalline materials and macroscopic forms. These reveal Thompson's clear-sighted view of the role of physical and mathematical sciences in biology, as well as his blind-spots.

KEYWORDS D'Arcy Thompson, biological form, patterns, morphology, liquid crystals, molecular biology

Introduction

This article samples contemporary thoughts on form in biological materials, and attempts to tease out the role Thompson has played — or missed — in colouring current thinking. The contemporary landscape of form, like the scope of *On Growth and Form* (Thompson 1942, hereafter abbreviated to *G&F*), is vast. A panoramic survey is therefore impossible. My study is governed by two factors. First, my understanding and familiarity of current research is constrained by my own curiosity, finite capacity, and specialized knowledge. Second, I view Thompson's legacy as a philosophical call to arms in how one approaches biology and morphogenesis. Every generation, possibly every reader, digests *G&F* in their own fashion, and I am no exception. My reading recognizes above all Thompson's evident comfort with mathematics and physics, a level of expertise that allowed him to write a text that repeatedly straddles both the biological and the physical worlds. More profoundly, he hints at a middle kingdom: a universe neither living nor dead, or one that is both.

Given his frequent dissatisfaction with aspects of Darwin's work, Thompson's writings in *G&F* have been dissected, praised and buried by numerous scientists whose allegiances lie in biology. Indeed, some of his most celebrated champions are Peter Medawar (1967) and Stephen J. Gould (1992),

DOI 10.1179/030801813Z.00000000030
Published by Maney on behalf of the Institute

who surely rank as giants of the biological sciences of recent decades. Nevertheless, I suspect their enthusiasm may be atypical. Thompson's biological universe could be equally interpreted as a quaint Victorian effort that ignored and/or rejected the looming juggernaut of genetics — as outmoded, say, as late-nineteenth-century physics before it was transformed by the revolution of quantum mechanics. Biology is now reshaped almost exclusively in the mould of molecular biology, and the Darwinian view reigns supreme. Contemporary understanding of biological systems relies almost exclusively on arguments of fitness and phylogeny, from the molecular scale of DNA to the collective behaviour of forest ecosystems. I witnessed the extraordinary outpouring of fervour for Darwin during recent sesquicentennial celebrations of his famed book with surprise and some hesitation. The tone occasionally approached church-hall revivalism, complete with fundamentalist activists,[1] such as Richard Dawkins, ready to cut down any challenges to the Darwinian orthodoxy.

But Thompson surely has a point. Genes and the drive to propagate may be the fuel, but where is the engine? After all, all organisms are constituted of the same chemical stuff — atoms and molecules — as the rest of the material universe. Supramolecular self-assembly, resulting in extraordinarily complex biological forms at the submicron scale, is the rule rather than the exception in abiotic mixtures of molecules and solvents not unlike those found in living bodies (Lehn 1995). Those forms, mostly unknown in Thompson's time, fit neatly into the dictionary of patterns explored by Thompson. Furthermore, it is axiomatic that form and function are inseparable twins. Thompson's appeal to many scientists lies in his implicit recognition of the form–function conjunction, now thoroughly accepted and driving much of the structural studies in molecular biology. He explicitly recognizes that all systems, living or dead, are subject to the forces at work in our universe.

In this study, I describe a selection of developments, principally from the broad school of materials science, that clarify the strengths and the weaknesses of Thompson's ideas. This discussion is ordered roughly according to characteristic length scale of the phenomenon from the subatomic to the macroscopic.

The (sub)atomic scale. Quantum mechanics and nuclear 'form'

Despite his own panoramic sweep of length scales in the biological universe, and his profound appreciation of the importance of scale in biology, Thompson remained uninfluenced by the revolution in quantum physics that swirled around him between the first and second editions of *G&F*. In his later version, he explicitly addresses those advances (Thompson, 1942, p. 20). Remarkably for a mid-twentieth century biologist, he considers briefly the possibility that quantum physics, active 'within a universe within which all Newton's is but a speck' may have a bearing on biology. He rejects that possibility, arguing that the 'world of the living, wide as it may be, is bounded by a familiar horizon... our scales of time and magnitude suffice'. A brief excursion into advances in quantum science suggests that the horizon of the living may conceivably extend into the quantum domain, though the reach remains speculative at best.

The fundamental monad of quantum science is the quantum state vector, whose evolution and interactions are governed by Schrödinger's wave mechanics. (Here I write 'evolution' in a non-Darwinian sense, despite

extraordinary claims of quantum Darwinism at work in the ecosystem of wave functions (Zurek 2009). Those claims can I think be safely ascribed to sesquicentennial euphoria.) Surely Schrödinger was aware of *G&F*, given that his seminal little volume of lectures, *What is Life?*, appeared just two years after the publication of Thompson's second edition of *G&F*. In that volume, the founder of quantum wave mechanics wrestles with related issues to those of Thompson, from the more abstract perspective of statistical physics and quantum mechanics.

Schrödinger's speculations on possible quantum effects in biology continue to preoccupy physicists, so far without decisive breakthroughs and to mixed reception. The major issue besetting any claim of quantum activity *in vivo* is one of quantum coherence — that is, maintaining an organized phase relationship between the wavefunctions of the constituent quantum entities. Whether coherence and associated effects such as entanglement (the interdependence of quantum states) can be maintained in warm, wet environments that characterize living organisms remains unclear at best (see, for example, Abbott *et al.* 2008), although quantum coherence has been reported in photosynthetic systems (Engel *et al.*, 2007, Lee *et al.*, 2007). A classical signature of the wave-particle duality inherent to quantum mechanics is the interference pattern produced by firing quantum particles through a double slit. Hornberger *et al.* (2003) have demonstrated that carbon fullerene molecules, which are huge objects from a quantum perspective, can exhibit this delocalization effect. Those findings hold some promise that quantum effects can indeed extend to relatively large length scales, commensurate with biological systems. However, those same experiments demonstrated the dissolution of the quantum nature of fullerene molecules, which revert to classical particles in the presence of gas. This is an illustration of how interactions between a coherent object and its surroundings rapidly induce decoherence, erasing all quantum effects. In my view, speculations on the role of quantum physics in the biological realm remain just that until (or unless?) a deep issue that besets much of biology is better understood: the role and effective structure of water *in vivo* (Ball 2008). Is it possible that water in biological systems, which is surely a distinct entity to bulk water, can effectively screen the usual decohering effects of temperature and exchanges with external systems, to maintain coherence? We do not know.

Perhaps unsurprisingly, the other revolution in twentieth-century physics — the discovery of the subatomic nucleus — was also ignored by Thompson. However, recent work has had a decisive influence on the vexed issue of biogenicity (the 'origin of life') and the nature of ancient life: nuclear isotopic abundance. This work explores the divide between the purely physical and the biological worlds, a no-man's land that Thompson urged scientists to explore in more detail. It has long been argued that biochemical processes (for example carbon fixation) favour lighter isotopes over heavier ones (^{12}C over ^{13}C, say), leading to ratios of heavy-to-light isotopes of carbon, sulfur and oxygen *in vivo* that are skewed compared with the physical background. This imbalance is then retained to some degree in fossilized remains, giving a potentially useful biosignature (O'Leary 1981). An increasing body of evidence, however, demonstrates substantial overlap (in the case of carbon isotopic fractionation) between the horizons of the worlds of the (once) living and the inanimate (McCollom 2003, McCollom *et al.* 2010). These painstaking studies reveal that abnormal abundance of light (^{12}C) carbon nuclei in reasonably complex organic molecules, both aromatic and aliphatic, is *not* confined to biochemical processes. So the putative biosignature maybe indeed be the result of biological activity, or may be effectively forged by

chemical processes devoid of any biological activity. This phenomenon certainly throws doubt on much work regarding fossil identification. At a more philosophical level, the scepticism surrounding the publication of this work, which I witnessed second-hand, surprised me. Had I recalled Thompson, I would not have been. Thompson writes 'In short, he is deeply reluctant to compare the living with the dead, or to compare by geometry or by mechanics the things which have their part in the mystery of life'. A century ago, when Thompson was writing *G&F*, vitalism was a largely accepted concept in scientific thought, explaining in one sweep the mysteries of the biological universe. That attitude, now largely antiquated, explains his polemic *a propos* geometry and mechanics. Though largely buried today, hidden vestiges of vitalism linger, colouring discussions to this day.

The molecular scale. Proteins, DNA and biopolymers

Surely the greatest revolution in biology since Thompson's time is the maturation of molecular biology, co-founded by the first generation of crystallographers, J. Desmond Bernal and William Astbury (Figure 1), both students of William Henry Bragg. Bernal's work on protein structure is relatively well-known. In contrast, Astbury's exploration of structural proteins are undeservedly neglected today. His diffraction studies of keratin, collagen, chitin, fibrogen, and globular proteins led to his naming of the α and β folds of proteins, and to key insights into the structures of the amino acids in DNA. His article 'The Form of Biological Molecules', written for a Festschrift dedicated to Thompson in 1945, outlines the foundations of modern molecular biology and remains a delightful and informative read (Astbury 1945) (in contrast, the other contributions to that volume have dated somewhat). He described his diffraction patterns from DNA as suggesting chain-like or columnar molecules, whose nucleotides are 'like a pile of plates in a tall plate stand' (Astbury 1945, p. 348). Although, like Thompson, he was sometimes incorrect in detail (Bernal 1963), his basic vision of the structural universe of proteins — that the amino acids govern the resulting protein conformation — and his notion that their structures are responsible for their function, from the extreme rigidity of chitin to the elasticity of keratins, hold true. By 1945, he already recognised the extraordinary importance and relevance of biomolecular structural studies ('First things first!', Astbury 1945, p. 325), particularly of proteins and nucleic acids: 'As we turn the pages of *Nature*, say, we see the need for information in this field growing weekly more urgent and the conviction growing ever more firm that with the nucleo-proteins lies far and away the greatest responsibility in all processes of growth and differentiation' (Astbury 1945, p. 351). Here we read the first enunciation of the great dogma of modern molecular biology, written eight years before Watson and Crick's double helix.

Thompson's neglect of molecular biology can perhaps be ascribed to his advancing age. Alternatively, it may reflect a more general disinterest in the early results of the new science of biomolecular crystallography. Crystallography is, after all, neither physics nor chemistry nor biology. Its peculiar position within the traditional scientific hierarchy was well expressed by Joseph Needham in 1932 in response to the views of J. B. S. Haldane: 'But here he neglects a figure who is always very much neglected in these discussions, namely, the crystallographer, who stands in some obscurity between the physicist on one hand and the biologist on the other' (Needham 1932). Crystallography was a new discipline, with no counterpart in the classical worlds of physical and geometric inquiry, so loved by Thompson.

FIGURE 1 (*a*) William (Bill) Astbury. (*b*) J. Desmond Bernal (below) and Joseph Needham (above) meeting at the Club for Theoretical Biology in Cambridge.

I cannot hope to survey the subsequent development of structural studies of proteins, viruses, and DNA here. The diffraction studies of biomolecules pioneered by Bernal, Astbury were later complemented by an equally powerful technique, electron microscopy, followed still later by NMR techniques. However, the major impetus to advances in biomolecular science has been the development of ever more powerful photon sources, from synchrotrons to x-ray free electron lasers, which allow smaller crystals to be explored and are capable of imaging crystals containing just a few molecules and collecting diffraction data at femtosecond time scales (Boutet *et al.* 2012). The Protein Data Bank (RCSB), downloadable today as a smartphone app, is a massive biological resource and a testament to the central role of protein structure in understanding modern biology.

It is becoming increasingly apparent, however, that protein regulation of biological functioning and activity is often mediated by the presence of lipids, which comprise the bulk of cell-bound membranes. The role of lipids was conceived initially as nothing more than a passive matrix, according to the Nicolson–Singer fluid–mosaic model of membranes (Singer and Nicolson 1972). The active intervention of lipids in mediating and activating protein interactions (and *vice versa*) has been suggested and explored repeatedly (Larsson and Rand 1973, Israelachvili *et al.* 1980, Pearson and Chan 1987, Hyde *et al.* 1997), leading to a more nuanced view of the relative importance of lipids. The classical fluid-mosaic model is now superseded by the lipid-raft model (Simons and van Meer 1988, Simons and Ikonen 1997). The latter model, which views the plasma membrane as a patchy, many-phase aggregate of biochemically distinct regions, imputes a strong biofunctional aspect to specific membrane lipids and proteins, aided by other important membrane-bound species such as cholesterol. Developments in understanding the complexity of lipid systems, deduced principally from liquid-crystal research

described in the following section, lend strong credence to this more refined view of biological membranes *in vivo*.

Molecular aggregates. Liquid crystals

Liquid crystals — a fourth phase of matter that hovers between the patterned arrays of crystals and the relatively formless molecular swarm that characterizes liquids — occupy an interesting role in Thompson's philosophy of form. His interest was triggered by the work of Friedrich Reinitzer and Otto Lehmann in the late nineteenth century, in which they uncovered intrinsic optical polarization (implying a degree of molecular orientational order) in a range of partially melted substances. The wriggling and growing textures of myelin (an aqueous extract from nerve sheaths, now recognised as composed of 'mesophases' of stacked lipid layers in excess water) viewed through the microscope by Lehmann were ascribed to the life force itself (*Gestaltungskraft*). He described these forms as 'artificial cells with liquid crystalline membranes' (translated in Sluckin *et al.* 2004, p. 564).

Lehmann's insight was surely ahead of its time: liquid crystals were largely unexplored until the 1960s, with the notable exception of Georges Friedel in France, who extended the findings of Lehmann and Reinitzer and described this state of matter as one quite distinct from liquids or crystalline solids. Friedel's careful microscopy studies led him to coin the term 'mesomorphism' to describe the multiple phases of liquid crystals (a term he eschewed), namely nematics, smectics and cholesterics (Friedel 1922). The subtle distinction between liquid crystals (a term eschewed by Friedel) and solids — evidenced for example by the way the former exhibit diffuse scattering of light rather than the Bragg diffraction obtained from fully ordered crystals — was, however, unclear to many scientists for decades, in part because crystallographic thinking was dominated by the views of Bragg and his successors, who implicitly conflated the concept of regular structure with that of diffraction. Thompson's reaction to Lehmann's finding of optical polarity in partially melted organic materials is representative of this flawed understanding of this new state of matter: 'a new conception is introduced when we find something like . . . space-lattices maintained in what has hitherto been considered the molecular freedom of a liquid field' (Thompson 1942, p. 731). This view remained for decades. For example, Thompson's champion Peter Medawar wrote in 1965 that the old conception of colloidal 'protoplasm' and 'its more sophisticated versions, which allowed for heterogeneity and for the existence of liquid crystalline states. . .' was inconsistent with the clearly visible structures detected in biological materials thanks to advances in electron microscopy. The credo of structuralism — championed by none other than Thompson — was a 'solid orderliness, indeed, for the so-called amorphous solids are either not really amorphous or not really solid' (Medawar 1967). Evidently, Medawar the biologist had not comprehended Friedel's detailed elaboration of the differences between mesosomorphs, liquid and crystals.

Today, we speak of two distinct classes of liquid crystals: thermotropics (which are formed by pure substances and exhibit liquid–crystalline phases on heating) and lyotropics (formed in 'solution', whose liquid-crystallinity is dependent on the volume of solution, such as water). Although conceptually flawed, Thompson's view of liquid crystals as almost crystalline applies reasonably well to lyotropics, and to some thermotropic phases (including smectic, blue and twisted grain boundary phases). However, the molecular

constituents of nematic and cholesteric thermotropic phases are not arranged in a translationally periodic lattice of any type; rather, they are *oriented* along the field lines of a three-dimensional vector field, and their locations are as random as those in a formless liquid (Figure 2). This orientational order is the origin of the peculiar polarization first noticed by Lehmann. Friedel likened the molecular arrangement in a nematic phase to a bag of needles; all more or less uniformly aligned, though lacking any positional order. It was therefore not surprising that previous attempts to classify the structures of liquid crystals — all done using nematics — failed to elicit any diffraction at all. Friedel suggested that smectics be studied with x-rays; one year later, his son Edmond Friedel and Maurice de Broglie succeeded in verifying (père) Friedel's layered model for smectics (de Broglie and Friedel 1923).

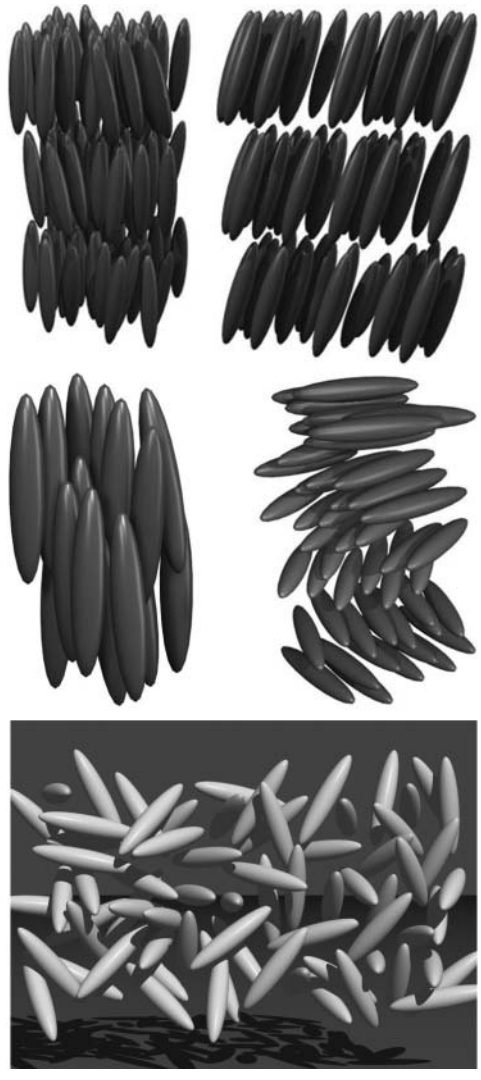

FIGURE 2 Liquid crystals are composed of molecules that are mobile and lack precise positional order, as in a liquid, but are orientationally ordered (*top*, smectic; *middle*, nematic; *bottom*, isotropic liquid). Images reproduced from Wikipedia.

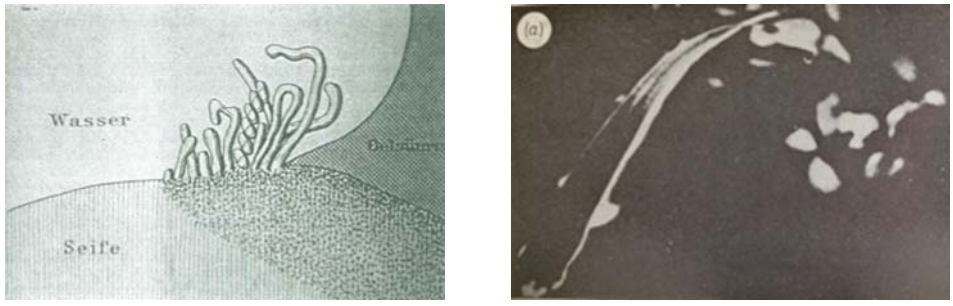

FIGURE 3 (*a*) Myelin figures observed by Lehmann. (*b*) Streaming birefringent solution of tobacco mosaic virus — visible in the eddies formed by a swimming goldfish (from Bawden *et al.* 1936). Photo reproduced with permission. (Copyright Nature Publishing Group.)

Liquid crystals *in vivo*

Some of the most significant advances in understanding biological form in recent decades are intimately related to the explosive growth in studies of both classes of liquid crystals, principally by physicists (thermotropics) and physical chemists (lyotropics). The ability of biological materials to form liquid crystals was first demonstrated by Bernal and coworkers in 1936 (Bawden *et al.* 1936), who demonstrated mesomorphism in suspensions of the rod-shaped tobacco mosaic virus, evident from both diffraction images and streaming birefringence (related to the optical polarization). An extraordinary image of the latter was produced, with streamlines formed by the action of a goldfish, swimming in a suspension of the virus encased between crossed polarizers (Figure 3). Before that, Lehmann surmised that natural myelins form liquid crystals. It is no surprise that Bernal first proved the existence of biological liquid crystals, given that he was a member, with Joseph Needham, of the celebrated Club for Theoretical Biology, based in Cambridge and founded in 1934–35. Bernal felt that biology must ultimately rest on physicochemical processes at the molecular scale. That view defines the dominant ethos of biology to this day. He argued that the spectrum of biological phenomena could be viewed as rungs on a hierarchical ladder, whose lowest rungs were atomic and molecular interactions and assemblies governed by quantum mechanics (Senechal 2012, p. 125). An integral seed in the musings of that extraordinarily ambitious group, surely sown by Bernal's laboratory studies, was the liquid-crystalline state.

Following Bernal's work, there followed decades of relative silence on the topic of biological liquid crystals. A notable exception was the industrial research of Conmar Robinson on (synthetic) polypeptide self-assembly (Robinson 1956). From the late 1960s, research into thermotropic liquid-crystalline materials grew rapidly, with particularly active centres in Hull, Paris VI (Orsay) and Kent State Universities. Research in Hull, led by George Grey, focused on new synthetic materials and ultimately led to the development of liquid-crystal displays. The Orsay group pioneered liquid-crystal physics. Their interests, however, extended to biological systems, with strong links to the French research community concerned with biological self-assembly, including Vittorio Luzzati and Yves Bouligand (Figure 4).

Bouligand's fertile explorations of biological form are without parallel in the modern post-Thompson era. Like Thompson, for whom he displayed the

FIGURE 4 (*a*) Yves Bouligand (image courtesy of Mme Bouligand). (*b*) Vittorio Luzzati with one of his personal photographs of Rosalind Franklin in the background. (Photo Philippe Plailly. Copyright, Look at Sciences, Paris.)

utmost respect (Bouligand 2011, p. 251), he was a man of very broad learning. The son of a celebrated mathematician and mathematical pedagogue, he began his career as a conventional zoologist, with interests in parasites and corals. Later, he explored a wealth of biological patterns using electron microscopy. The range of biostructures he explored (together with his long-standing team of Françoise Livolant, Françoise Gail and Marie-Madeleine Giraud-Guille) reflects his intense interest in morphology *in vivo*: from the packing of DNA in chromosomes to the envelopes of fish eggs, and hard cuticles of various species from crustaceans, insects, spiders to worms (Bouligand 2011, p. 53). To his great surprise, he detected similar fibre textures in all of these materials. These fibres — whether of hard structural chitin or threads of DNA — had all been explored at the atomic scale by Astbury *in vitro* thirty years earlier without the advantage of an electron microscope. In contrast to the crystalline packings Astbury inferred, Bouligand found a common pattern of nested arcs aligned along ribbons. 'With a little bit of geometry' (Bouligand 2011, p. 51), he inferred that these arcs were indicative of oblique sections through twisted plywood-like layers of parallel fibres, where the orientation of the fibres rotates slowly from layer to layer. A simpler 'two-ply' pattern, with layers rotated an almost fixed angle relative to their neighbours, had in fact been reported by Astbury in his study of the cellulose fibre decoration of giant cells of *Valonia*. (It is curious to note that this study by Astbury led to a detailed discussion in the 1942 edition of *G&F*, although deeper principles of protein structure and biological assemblies enunciated by Astbury and Bernal were ignored there.) In contrast to the two-ply pattern, Bouligand detected a pattern with quasicontinuous rotation. The single twist of adjacent molecules, screwed along one axis according to a continuous vector field just as seen in synthetic cholesteric liquid crystals, was utterly novel. Shortly after his initial reports, Bouligand was contacted by Conmar Robinson, who had seen the same patterns in his synthetic polypeptide cholesterics and DNA dispersions. Unlike Bouligand, Robinson recognised these as the cholesteric thermotropic structures

suggested by Friedel. Naturally, Bouligand turned to his physicist colleagues in Orsay and was soon in the forefront of liquid-crystal research, publishing in both physics and biology journals.

Bouligand's discovery of thermotropic cholesterics is a significant advance on Thompson's work. The fibre mapping of his discovery of *Valonia* cell walls by Astbury, discussed by Thompson in terms of curved geodesics, pales into insignificance compared with Bouligand's account of cholesteric ordering (a kind of helical orientational order). First, the widespread occurrence of these patterns, from DNA in chromosomes to spider and crustacean carapaces, is extraordinary. Secondly and more importantly, the findings immediately suggest a simple morphogenesis for these structures: biomolecular self-assembly. Studies have confirmed that chitin can self-assemble *in vitro* to form cholesteric arrays in aqueous suspensions, not unlike those observed *in vivo* (Belamie *et al.* 2004). The case for self-assembly of DNA *in vivo* is equally compelling, with strong similarities to cholesteric liquid-crystalline assemblies observed *in vitro* (Livolant 1991).

Subsequent work led to tantalizing suggestions that liquid crystals are yet more widespread in biological organs and organelles, lending further support to the hypotheses of Bernal and Needham. For example, a prime mover of liquid-crystal research in the United States, Glenn Brown, co-authored an entire volume exploring the occurrence of liquid crystals in biological organisms (Brown and Wolken, 1979). This monograph contains micrographs of a number of biological structures in photoreceptors, visual systems and membranes, whose structures appear to adopt liquid-crystalline phases of proteins and/or lipids. Structural similarities to both thermotropic and lyotropic mesophases are evident. *In vitro* lyotropic phases with membrane-forming molecules such as lipids and membrane proteins in water identified at that time included lamellar and hexagonal phases, made of layered flat sheets and close-packed rods respectively. The potential relevance of these phases to biological structures observed *in vivo* had in fact already been flagged in the early 1960s by Luzzati, following his pioneering studies of lipid-water mesomorphism (Luzzati and Husson 1962).

A noteworthy omission from Brown and Wolken's survey (which was apparently done in splendid isolation of all other work, including that of Luzzati and Bouligand) was the extraordinarily complex patterns observed by Brian Gunning, a botanist who investigated plant chloroplasts, the engine of photosynthesis. Gunning described peculiar structures found in prolamellar bodies, the precursors to choloroplasts (Gunning 1965). Here the lipid membrane was not sheet-like. Rather, it formed a three-dimensional porous network of lipid multilayers with close to ideal cubic symmetry, and lattice parameters (that is, periodicity) of the order of 50–100 nm. Later work by Gunning revealed a variety of different tubular networks, some related to the crystal structures of (cubic) inorganic compounds and others apparently aperiodic (Gunning and Steer 1996).

These exotic patterns, whose topology is far more complex than those of the 'classical' lamellar and hexagonal liquid-crystalline phases, were recognised by Kåre Larsson (Figure 5) and Israelachvili *et al.* as close relatives of the mathematical entities called three-periodic minimal surfaces (Figure 6), as well as of (then novel) lyotropic liquid crystals known as bicontinuous cubic phases (Larsson, Fontell and Krog 1980, Israelachvili and Wolfe 1980, Larsson and Anderson 1986). In addition, Larsson and Andersson noted the resemblance of a plasma membrane in the intestinal wall of an insect (Lane and Harrison, 1979) to periodic minimal surfaces. The beauty of minimal surfaces — 'minimal' because they have minimal surface area and zero mean

FIGURE 5 Kåre Larsson (image courtesy Kåre Larsson).

curvature — is undeniable, and can be seen in soap films, favourite toy models of Thompson for biological morphologies. His own description of the macroscopic undulating membranes of a trypanosome is an accurate, if characteristically poetic picture, of these surfaces: 'the membrane, for every alteration of its curvature must at the same instant become curved in a direction perpendicular thereto; it bends... with the accompaniment of beautiful but tiny waves of double curvature, all tending towards the establishment of an "equipotential surface", which indeed, as it is under no pressure on either side, is really a surface of no curvature at all' (Thompson 1942, p. 432). Shortly thereafter, Larsson *et al.* demonstrated that the minimal surfaces called the gyroid and D-surface accurately described two distinct bicontinuous cubic phases observed in lyotropic liquid crystals *in vitro*, formed by a simple lipid–water mixture (Hyde *et al.* 1984). These anticlastic surfaces form sponge-like patterns, and bisect space into a pair of interpenetrating but mutually isolated three-dimensional networks (whence 'bicontinuous'). A similar phase had been reported earlier by Luzzati and Spegt, formed in a dry (and hence thermotorpic) soap (Luzzati and Spegt 1967). These bicontinuous phases might perhaps be better described as a pair of threaded nets, and have been commonly encountered in recent years in crystals synthesized from organic molecules linked by metal ions (Batten and Robson 1998).

Since these preliminary suggestions of bicontinuous cubic structures existing *in vivo*, a wealth of evidence verifying that notion has been collected, primarily by Larsson and Tomas Landh (Hyde *et al.* 1997, Landh 1995 and

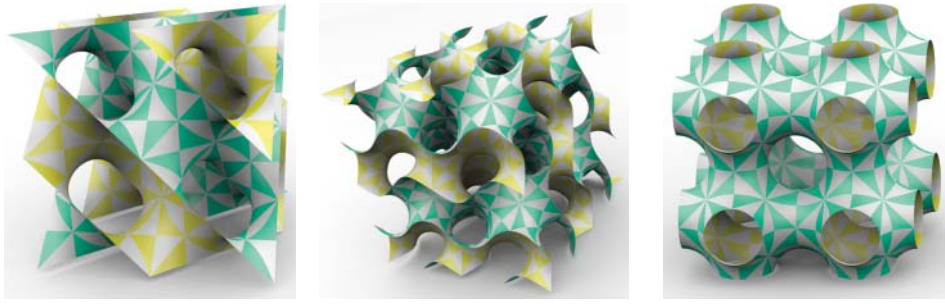

FIGURE 6 The most common periodic minimal surfaces: (*a*) the D- or diamond surface, (*b*) the gyroid and (*c*) the P- or cubic surface. Images courtesy of Myfanwy Evans, Friedrich-Alexander Universität Erlangen-Nürnberg.

FIGURE 7 Alan Schoen on the roof of the Courant Institute, New York, holding his model of the gyroid. (Photo courtesy of Stefan Hildebrandt.)

Yuru Deng (Almsherqi *et al.* 2006). So far nearly all of these membranes adopt the geometries of the cubic gyroid, D- and P-surfaces.[2] Thompson would be impressed with their geometric character: these 'cubic membranes' correspond to the most symmetric hyperbolic surfaces commensurate with three-dimensional Euclidean space, and hence the closest analogues to the ideal surface of constant negative curvature. The scientific relevance of these structures beyond obscure complex function theory and classical differential geometry was unknown until mathematician Alan Schoen's discovery of the gyroid (Schoen 2012; Figure 7) and subsequent interest from physical scientists since the 1980s (Hyde *et al.* 2008). Curiously, many examples of these membranes appear under pathological conditions, from virus infection in higher animals to light starvation in plants. These situations are invariably associated with abnormal protein contents (overexpression of specific antigens in the presence of viruses and underexpression of typical proteins in the absence of light). Given that these structures appear *in vitro* in chemically monodisperse (single-component) systems only (polydispersity allows the phases to melt, forming disordered lyotropic 'sponge' phases), this observation suggests strongly that their morphogenesis is governed by molecular self-assembly *in vivo* also.

Despite the strong structural resemblance between bicontinuous cubic phases *in vitro* and cubic membranes *in vivo*, it is important to point out that the latter structures are typically an order of magnitude more swollen than the former — in other words, the length scale of the cubic lattice is larger. No physical mechanism is known that allows bicontinuous cubic phases to swell to the extent seen in most biological systems. A notable exception is the plasma membrane of the archaebacterium *S. solfataricus* (Luzzati 1997). Here, electron microscopy has revealed an extraordinary lattice of protein embedded in the lipid membrane, forming a two-dimensional slice through the D-surface just as adduced by the model advanced by Larsson (Larsson and Andersson 1986, Larsson 1989). Aside from this example, however, the enormous size of cubic membranes compared with cubic phases remains a challenge to explain. Until that happens, we are unable to conclude definitively that cubic membranes form *in vivo* through self-assembly, likely as that seems.

The functions of these structures are frankly unknown, despite a number of intriguing hypotheses regarding the efficacy of sponge-like membranes

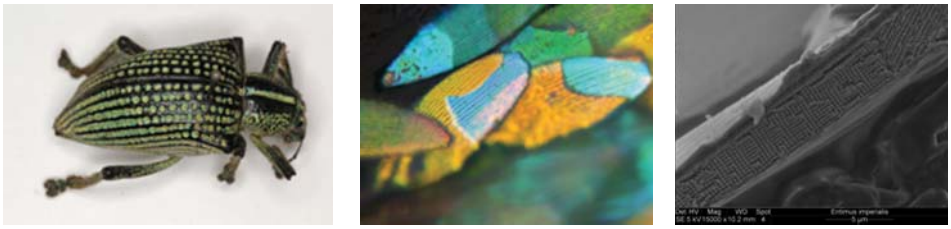

FIGURE 8 Structural colour in the diamond weevil: (*a*) the weevil; (*b*) optical micrograph of coloured scales in the cuticle; (c) scanning electron micrograph of the interior of a scale. The spots in the cuticle contain chitin networks forming a single dia (diamond) net, affording *post-hoc* justification for its common name! All images by Bodo Wilts, reproduced courtesy of Wilts.

(for example, as optimal photon traps) compared with more usual lamellar arrays (see, for example, Almsherqi 2006). One particularly striking function does, however, deserve note: the formation of photonic crystals via cubic membranes. These objects have characteristic length scales of the order of the wavelength of light, and interact with visible light to produce 'diffraction colours'. The control that they offer over the transmission of light might lead to applications in optical computing. Their dimensions are huge compared with atomic and molecular scales — of the order of a few thousand atoms thick — and their probable formation by self-assembly is an impressive feat of nature. Biologists have long known of many instances of 'structural colour' in insects and birds (Onslow 1923) (Figure 8), though the structural origin of these complex patterns had been a matter of heated debate. Electron microscopy has now clarified the structures considerably. Recent work has identified easily recognisable cubic network structures within the interior volume of insect cuticles (the 'procuticle'), in a range of insects from butterflies to weevils. For example, wing scales of the European Green Hairstreak butterfly (*Callophrys rubi*) contain a complex network of the fibrous protein chitin, formed in small grains within individual scales on the wing (Figure 9, Morris 1975). Their geometry is precisely that of one network formed by the gyroid or the D-surface (Michielson and Stavenga 2008,

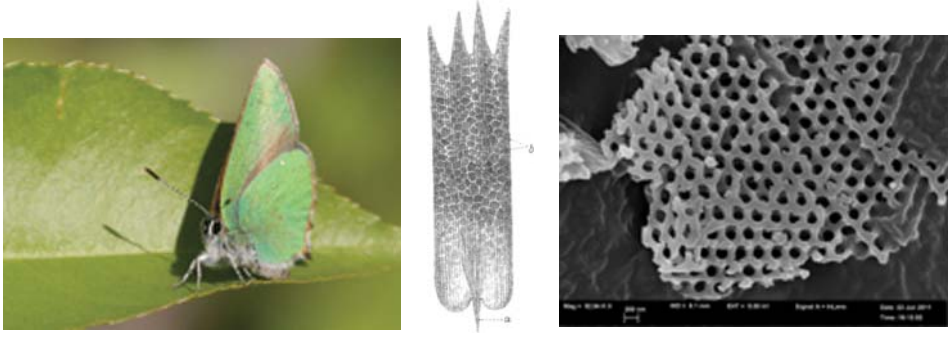

FIGURE 9 (*a*) Under-wing colour in the Green Hairstreak butterfly (*C.* rubi) attributed to coloured grains within (*b*) wing scales (optical micrograph from Onslow 1923). (*c*) Scanning micrograph showing a fragment of the structured srs chitin network in a single grain. Images: Onslow, Carnerup.

Saranathan *et al.* 2010, Schröder-Turk *et al.* 2011, Wilts *et al.* 2011), namely the so-called srs and dia (diamond) nets,[3] respectively. Both the D- and gyroid structures function as photonic crystals, resulting in brilliant spots of colour on the cuticle, typically varying from blue to green depending on the exact dimensions and orientation of the chitin net.

These patterns are morphologically identical to those found in bicontinuous cubic lyotropic liquid crystals, rather than the cholesteric thermotropic mesomorphs found by Bouligand. This is odd: the procuticle is largely chitin, a fibrous protein first explored by Astbury and known to self-assemble into cholesteric structures. Painstaking morphological studies by Helen Ghiradella have explored the scale development in the wet conditions of the larval test.[4] Her work revealed the presence of cubic membranes in the smooth endoplasmic reticula of scale cells. So here, a cubic pattern is formed by the membrane lipid and proteins, as explored by Landh and Deng *et al.* (Landh, 1995, Almsherqi et al., 2006). Ghiradella's studies revealed that the chitin slowly crosslinks in one of the two disconnected spaces generated by the membrane folding. Thus, the soft membrane acts as a template for the extraordinary chitin networks (Ghiradella 1989). The details of this templating process remain unknown, but it is clear that this extraordinary pattern emerges from cubic membranes analogous to the bicontinuous cubic mesomorphs seen *in vitro.* The mechanism is undoubtedly biochemically complex in detail yet simple in plan, and is a remarkable example of the efficacy of self-assembly in building structures at optical length scales, with tens of thousand of molecules aggregating under the influence of weak interactions to form the jewel-like structures visible to the naked eye.

Our understanding of the morphogenesis of coloured bird feathers is less complete. Thompson accurately describes the ultrastructure of one coloured feather thus: 'The jay's blue feathers shews a layer of enamel-like cells beneath a thin horny cuticle and the cell walls are spongy with innumerable tiny air-filled pores' (Thompson 1942, p. 55). In many (though not all) cases, structural colour is produced by a complex network of keratin protein, topologically similar to the networks in butterfly and weevil epicuticles, but geometrically very different. In other examples, disordered spherical inclusions of air appear in a continuous keratin matrix (Noh *et al.* 2010). In contrast to the crystallographic patterns found in weevil and butterfly cuticles, the feather network is not crystalline but disordered (Figure 10). A plausible, though unproven, explanation for their morphogenesis lies in their templating from membranes whose folding is strongly reminiscent of yet another lyotropic liquid-crystalline mesophase, the 'sponge phase', closely related to bicontinuous cubic phases (Hyde 2001). Although non-crystalline, sponge phases are in fact sufficiently ordered to act as photonic crystals, producing a rich palette of colours in many birds.

A variety of more or less complex chitin and keratin patterns has been detected in insects, birds, and higher animals. It is surely not coincidental that — like the bicontinuous cubic and sponge phase examples above — all patterns seen *in vivo* match the geometries of water channels in lyotropic liquid-crystalline phases found *in vitro* (although the protein assemblies are an order of magnitude more swollen). A couple of examples beyond the bicontinuous cubic and sponge phases from our own work demonstrate the point. The first is found in the spectacularly hued Madagascan Sunset moth (*Chrysiridea riphea*) (Figure 11). Here a common morphology is observed for a range of coloured wing scales, from red to blue (with varying dimensions): laminae of chitin separated by chitin pillars arranged in a quasi-hexagonal array (Carnerup *et al.* 2012). This structure mimics that of the water matrix of

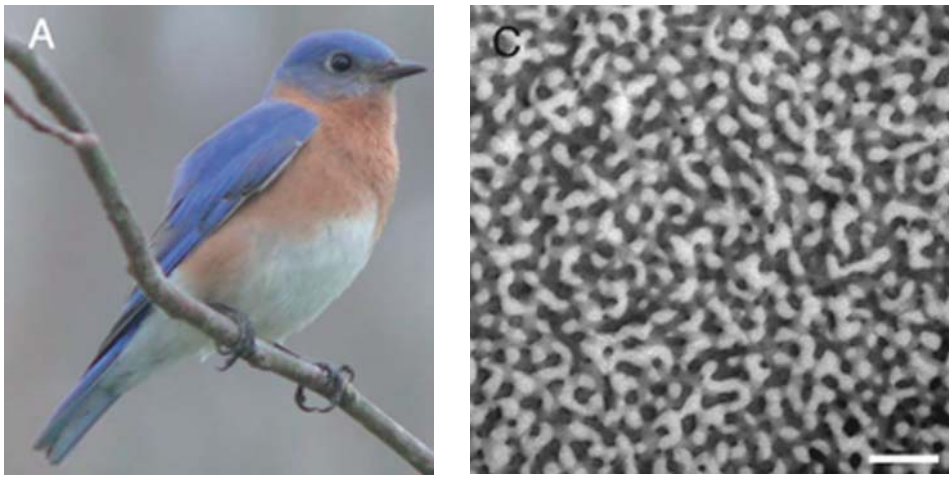

FIGURE 10 (*a*) A male Eastern Bluebird (*Sialia sialis*). (Photo by Ken Thomas, in the public domain). (*b*) The random sponge-like matrix of keratin observed within back contour feather barbs, leading to the bird's brilliant blue coloration. (Scale bar 500 nm.) (Reproduced courtesy of Richard Prum (Dufresne et al., Soft Matter, 2009 5: 1792–179; http://dx.doi.org/10.1039/B902775K. Reproduced by permission of The Royal Society of Chemistry.))

a lesser known lyotropic liquid-crystalline phase discovered by Luzzati and co-workers, the rhombohedral phase (Hyde 2001). The second is an idealized structure that probably corresponds to the packing of keratin filaments in the outermost layer of mammalian skin (the *stratum corneum*). This structure, similar to the chitin network in wing scales, lies tightly within one channel of the gyroid pattern, suggesting that it too is formed by a template of a cubic membrane *in vivo* (Evans and Hyde, 2011).

A cautionary note is in order here. Although these patterns indeed mimic equilibrium liquid crystals formed *in vitro*, it is probable that their biogenesis is a more complex story. Given the confined conditions and varying physicobiochemical environment in which these structures are synthesized *in vivo*, direct mapping between the biological and laboratory materials is

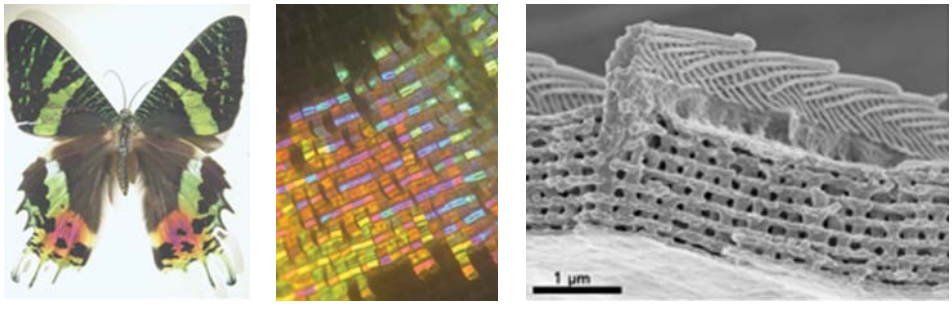

FIGURE 11 (*a*) The Madagascan Sunset Moth (*C. riphea*). (*b*) Optical micrograph of a wing showing multicoloured wing scales. (*c*) Scanning electron micrograph within a wing scale, showing a laminated chitin pattern, with pillar separating adjacent laminae (Electron micrographs courtesy of Anna Carnerup).

unlikely. It is clear for example, that biological function — essentially a massively parallel physicochemical machine — depends on the maintenance of concentration gradients and effective compartmentalization. Although biological environments are rarely, if ever, in thermodynamic equilibrium, one may think of morphogenesis *in vivo* as arising via local quasi-equilibrium conditions, varying in time and space. That implicit assumption underlines the utility of molecular self-assembly as a structure-building principle in biology over at least three orders of magnitude: from the atomic structure of small globular proteins to the micron-scale patterns in higher animals. The principal forces driving all of these assemblies, beyond chemical bonds, are hydrophobic interactions. Thompson's concept of a structure as a 'diagram of forces' is confirmed without exception by these assemblies.

On form and growth at the multicellular scale. 1 Synthetic biology and living inorganic matter?

The startlingly simple *leitmotiv* of *G&F* — that biological form is moulded by the interactions of the organism and its constituents with the physical world — naturally leads Thompson to repeatedly pose the question of whether there are differences between biological morphologies and the shapes found in inanimate matter. In the course of a discourse on the immutability of physical forces over time, he writes without a hint of ambiguity: 'A snow-crystal is the same to-day as when the first snows fell'. If evolution is an essential trait of biological life, snowflakes are archetypal inanimate objects. Since Thompson's time, there have been many attempts to define life in the most general sense — far too many to canvass in any detail here. Modern concepts of complexity and emergence are just two of the most recent concepts that capture aspects of many living systems (Capra 2005). These characteristics, like many others, are generally judged to be deficient, in that they also admit all manner of dead objects, from computer programs to sand dunes. Indeed, the usual criteria for life found in innumerable undergraduate biology textbooks are fulfilled by crystals too, from snowflakes to steel. This problem is central to many areas of science. For example, the search for life on Mars and elsewhere is futile without agreement on what constitutes life. For unless that life is exotic and unknown on Earth, how can we exclude the possibility that it was transplanted from Earth, either by cosmic impacts or by direct transport aboard a human vehicle, many of which have already left their tell-tale deposits of bacteria on Mars? The massive research effort in synthetic biology (see, for example, http://syntheticbiology.org/) demands commensurate deliberations on what constitutes life (Deplazes and Huppenbauer 2009). It is clear that a clear scientific distinction between living and inanimate matter remains very unclear.

Nowhere is this better illustrated than the current debate surrounding the fossil evidence for traces of the most ancient terrestrial life. Septated filamentous structures detected in carbonate inclusions in well-preserved Archean rocks in northwest Australia are widely assumed to be among the earliest forms of life on Earth. These 'microfossils' are around 3.5 billion years old — barely 1 billion years after the accretion of the Earth into a dense planet — suggesting the emergence of terrestrial life from at least that date (Grotzinger 1994). The primary evidence for biogenesis of these fossils is their microstructure, which indeed resembles contemporary filamentous bacteria, with curvilinear walls and chambers typical of simple multicellular life. To put it bluntly: these inclusions look biological, so it is assumed that they are.

Certainly, the forms are not the discretely faceted polyhedral shapes that characterize typical carbonate minerals. However, laboratory experiments show that precipitates of carbonate minerals in the presence of small quantities of silica are often filamentous, whose forms are remarkably reminiscent of these microfossils (García-Ruiz *et al.* 2003). The possibility that these celebrated Archaean-era inclusions are nothing more than inorganic matter, although demonstrably consistent with the geochemical environment of the host rocks, remains somewhat unacknowledged by many palaeontologists of the ancient Earth, who have spent decades developing careful 'biosignatures' based, in part, on morphological characteristics of biota. That approach is, in the light of the precipitation experiments, fundamentally flawed. As Thompson saw clearly, there is substantial common ground between the organic and inorganic worlds, and unless those commonalities are explored in more detail, much-trumpeted searches for ancient life on Earth, or life elsewhere, must be treated with caution.

That intermediate terrain is probably broader in scope than imagined. For example, a long-held alleged biosignature is that of chirality: numerous biologically important molecules, from sugars to amino acids, are synthesized *in vivo* in just one of two possible mirror-image forms (enantiomers). However, this reasoning too is flawed. For example, a recent study revealed that bacteria produce right-handed as well as the more common left-handed enantiomer of various amino acids (Lam *et al.* 2009). The search for biosignatures from the multi-cellular to the molecular level may ultimately prove to be a very subtle exercise. This commonality of living and nonliving matter is now known to extend to the tiny dimensions of the atomic nucleus: the commonly assumed isotopic fractionation effected by biological life is, as discussed earlier, also a chimera.

Despite repeated rejection and then rebadging, vitalism or Lehmann's *Gestaltungskraft* remains a working concept and governs much of modern society's thinking. The old duality between organism and machine persists. It is refreshing, and important, to absorb Thompson's views here. The numerous parallels between synthetic liquid crystals and cell organelles, biomorphs and bacteria surely confirm Thompson's still radical view that there are numerous parallels between the living and the inert, and updated versions of vitalism — any attempt to accord living systems a privileged status — are doomed to fail. As Thompson wrote almost a hundred years ago, 'The search for differences or fundamental contrasts between the phenomena of organic and inorganic, of animate and inanimate things, has occupied many men's minds, while the search for community of principles or essential similitudes has been pursued by few; and the contrasts are apt to loom too large, great though they may be' (Thompson, 1942, page 7).

On form and growth at the multicellular scale. 2. Macroscopic morphologies

The fundamental vision of Thompson in *G&F* is nowhere better expressed than in this way: '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. . . . Their problems of form are in the first instance mathematical problems, their problems of growth are essentially physical problems' (Thompson, 1942, loc. cit.). Realization of this claim is emerging for a number of biological forms at the macroscopic scale.

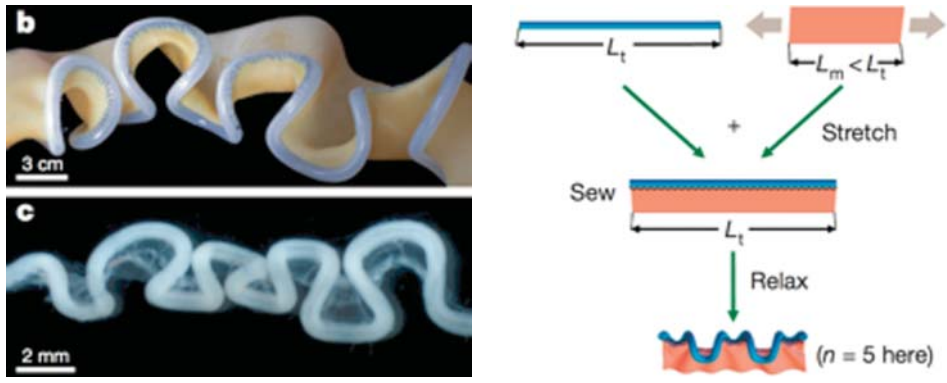

FIGURE 12 Morphogenesis of a chicken gut: (*a*) a model elastic composite containing a film attached to a fibre, both under tension; (*b*) a membrane attached to such an elastic fibre; (*c*) a chicken gut. (Images reproduced courtesy of Savin *et al.* (2011), Photo reproduced with permission. (Copyright Nature Publishing Group).

A first example is that of the developing gut in higher animals, from birds to mice. The shape of the gut is characterized by a complex sequence of ruffles, attached to a central gut tube. Here, both the development in the embryo and the shape of the mature form is readily explained in terms of an area mismatch between two attached elastic films: one comprising the tube lining the gut and the dorsal desentary (Savin *et al.* 2011). Remarkably, the number, shape and size of crenellations in the gut can be predicted from the model of Savin *et al.* across a range of species (Figure 12).

Almost thirty years ago, the geometer and topologist William Thurston wrote, in response to an inquiry about hyperbolic geometry by my then supervisor, Sten Andersson, that we should think about the 'shapes of leaves'. Understanding of these forms has matured considerably in the past few years. A rich spectrum of intrinsically curved forms can be traced to differential rates of growth in various directions. This concept, for example, directs the shapes of leaves. An elegant technique for analysing leaf curvature is to measure the radius of a flattened strip excised from the leaf (Sharon *et al.* 2007). This technique reveals that common bay leaves have a variety of curved forms, even from the same tree, from almost constant negative Gaussian curvature (Figure 13a) to increasingly negative Gaussian curvature from the stem to the growing edge (Figure 13b).

The technique allows the metric of a leaf (assumed to be a two-dimensional object) to be deduced empirically. This quantity is related to cell proliferation in different directions, and can be calculated if the cell size is known as a function of age, affording useful input to biological growth models. At present, the regulation of cell proliferation during growth is unclear, although it is an active research area. Here we see that differential geometry combined with clever, almost trivial, experiments goes part of the way to closing the gap between cell biology and morphogenesis.

A final example of form at the macroscopic level is that of flowers. The evolving form of a lily during blooming has been explained in engineering terms, in a study infused with the spirit of Thompson (Liang and Mahadevan 2011). As with the bay leaf example, the experiments to test competing hypotheses here owed nothing to twentieth-century instrumentation: a

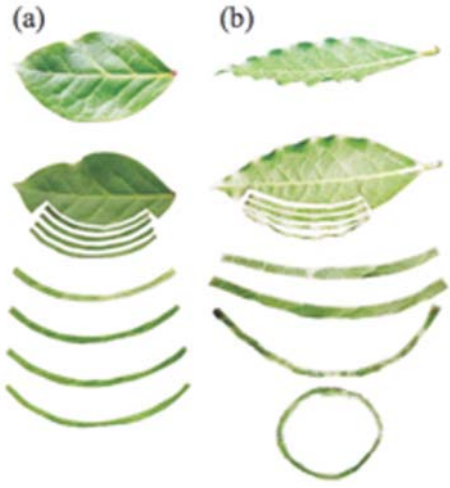

FIGURE 13 Gauging the intrinsic metric of bay leaves by excising strips and flattening :(*a*) the leaf is roughly homogeneous from stem to edge; (*b*) the leaf exhibits increasing curvature towards the edge. Image reproduced with permission of the authors (Sharon *et al.* 2007). Copyright 2007 American Physical Society.

humble scalpel is all this is needed. The blooming lily, which involves a reversal of curvature (positive to negative) from a closed bud to the characteristic trumpet form, as well as the crenellations around the petal perimeter, are shown by Liang and Mahadevan to emerge as minimizers of the bending energy of the petal, modelled as a slightly thickened shell (Figure 14). The blooming process is therefore nothing more than deformation of a flexible shell subject to anisotropic growth processes. Again, however, the essential input to the physical problem (the relative growth rate of the petal)

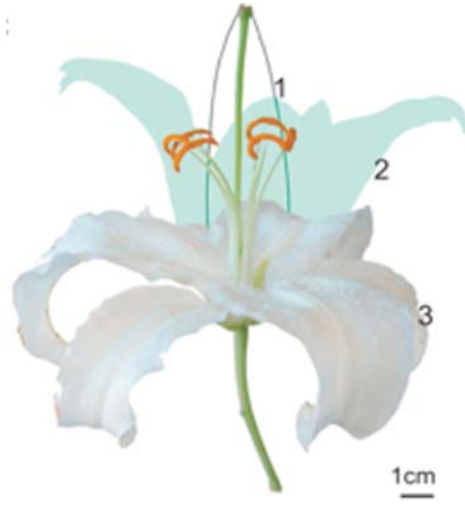

FIGURE 14 The flowering process of a lily, from the convex form of the closed bud (1) to the full bloom (3). Image reproduced courtesy of the authors (Liang and Mahadevan 2011).

is empirical, and as yet we have little idea of the details of that process of cell proliferation, although some progress has been made (Nath *et al.* 2003).

Mechanics and geometry can explain the genesis of multicellular forms in terms of differential growth in different parts of a leaf or a gut, but how are these growth rates so finely tuned? In order to realise Thompson's vision fully, better understanding of biological control of growth is needed. The spatial control of cell proliferation remains largely a mystery. Is it controlled at a genetic level by specific proteins (Nath *et al.* 2003), or — to adopt a view that Thompson surely would have preferred — via mechanical feedback as a result of the bending and stretching stresses within the growing object (Liang and Mahadevan 2011)?

Conclusion

This cursory survey of form suggests that the program undertaken by Thompson remains an active one. Although there is surely no longer doubt about the importance and relevance of genetic control of form in morphogenesis, the active intervention of mechanical and other stresses in a growing organism play an important part, from the opening and closing of protein channels to the beauty of a flowering bud.

Acknowledgement

I am very grateful to Zoltan Blum (Malmö), Anna Carnerup (Canberra), John Goodby (Hull), Kåre Larsson (Bjärred), Vittorio Luzzati (Orsay), Mahadevan (Harvard), Richard Prum (Yale) and Bodo Wilts (Groningen) for material assistance, advice and helpful discussions.

Notes

[1] See, for example, Dawkins' refusal to counter problems with Darwinism articulated by Simon Conway Morris, expressed with characteristic venom in a discussion on Darwinism (Open University Lecture 2009).

[2] With the exceptions of some of Gunning's structures, that remain unidentified, and the bilayer formed by (rabbit) lung surfactants *in vivo* that form a tetragonal minimal surface (Larsson *et al.* 2003).

[3] see http://rcsr.anu.edu.au/rcsr_nets

[4] The experimental stamina of biologists is impressive. Until I read Onslow's paper, I assumed Ghiradella's painstaking observations of developing wing scales were unique. They are not; Onslow also explored the development of colour in *C. rubi* (Onslow 1923, 45–46) without success. Without higher-powered microscopy, the structural developments in the pupa were impossible to discern.

References

Abbott, Derek, Paul C.W. Davis, and Arun K. Pati, eds. 2008. *Quantum aspects of life*. London: Imperial College Press.

Almsherqi, Z., S. D. Kohlwein, and Y. Deng. 2006. Cubic membranes: a legend beyond the Flatland of cell membrane organization. *J Cell Biol* 173: 839–844.

Astbury, W. T. 1945. The forms of biological molecules. In *Essays on growth and form presented to D'Arcy Wentworth Thompson*, ed. W. E. Le Gros Clark and P. B. Medawar, 309–354. Oxford: The Clarendon Press.

Ball, P. 2008. Water as an active constituent in cell biology. *Chem Rev* 108: 74–108.

Batten, S. R. and R. Robson. 1998. Interpenetrating nets: ordered periodic entanglement. *Angew Chem Int Ed Engl* 37: 1461.

Bawden, F. C., N. W. Pirie, J. D. Bernal, and I. Fankuchen. 1936. Liquid crystalline systems from virus-infected plants. *Nature* 138: 1051–1052.

Belamie, E., P. Davidson, and M. M. Giraud-Guille. 2004. Structure and chirality of the nematic phase in α-chitin suspensions. *J Phys Chem B* 108: 14991–15000.

Bernal, J. D. 1963. William Thomas Astbury. *Biog Mem Fell R Soc* 9: 1–35.

Bouligand, Y. 2011. Levels of organisation and morphogenesis from the perspective of D'Arcy Thompson. In *Morphogenesis. Origin of patterns and shapes*, eds. Paul Bourgine and Annick Lesne. Berlin: Springer Verlag.

Boutet, S. *et al.* 2012. High-resolution protein structure determination by serial femtosecond crystallography. *Science* 337: 362–364.

M. de Broglie, E. Friedel, C. R. Acad. Sci, Paris 1923, I76, 738.

Brown, G. H. and J. J. Wolken. 1979. *Liquid crystals and biological structures*. New York: Academic Press.

Capra, F. 2005. Complexity and life. *Theory, Culture & Society October* 22: 33–44.

Carnerup, A., S. T. Hyde and B. Wilts, 2012. In preparation.

Deplazes, A. and M. Huppenbauer. 2009. Synthetic organisms and living machines: Positioning the products of synthetic biology at the borderline between living and non-living matter. *Syst Synth Biol* 3: 55–63

Engel, G. S. *et al.* 2007. Evidence for wavelike energy transfer through quantum coherence in photosynthetic systems. *Nature* 446: 782–786.

Evans, M. E. and S. T. Hyde. 2011. From three-dimensional weavings to swollen corneocytes. *J Roy Soc Interface* 8: 1274–1280.

Friedel, G. 1922. Les états mésomorphes de la matière. *Ann Phys* 18: 273–474. Partial translation in *Crystals that flow*, ed. T. J. Sluckin *et al., loc. cit.*

García Ruiz, J. M., S. T. Hyde, A. M. Carnerup, A. G. Christy, M. J. Van Kranendonk and N. J. Welham. 2003. Self-assembled silica-carbonate structures and implications for detection of ancient microfossils. *Science*. 302:5648, 1194–1197.

Ghiradella, H., 1989. Structure and development of iridescent butterfly scales: Lattices and laminae. *J Morph* 202: 69–88.

Gould, S. J., 1992. This was a man. Foreward to *On Growth and Form, abridged Canto edition*. Ed. J. T. Bonner. Cambridge University Press.

Grotzinger, J. P. 1994. *Early Life on Earth.* New York: University Press, p. 245.

Gunning, B. 1965. The greening process. In Plastids. *Protoplasma* 60: 111–130.

Gunning, B. E. S. and M. Steer. 1996. *Plant cell biology*. Sudbury MA: Jones & Bartlett Learning.

Hornberger, K. S. Uttenthaler, B. Breezger, L. Hackermuller, M. Arndt and A. Zeilinger, 2003. Collisional decoherence observed in matter-wave interferometry. *Phys Rev Lett* 90: 160401.

Hyde, S. T., S. Andersson, B. Ericsson and K. Larsson. 1984. A cubic structure consisting of a lipid bilayer forming an infinite periodic minimal surface of the gyroid type in the glycerolmonooleate water system. *Z Kristallogr* 168: 213–219.

Hyde, S. T., S. Andersson, Z. Blum, S. Lidin, K. Larsson, T. Landh and B. W. Ninham. 1997. *The language of shape.* Amsterdam: Elsevier Science B.V.

Hyde, S. T. 2001. Identification of lyotropic liquid crystalline mesophases. In *Handbook of Applied Surface and Colloid Chemistry*. Ed. K. Holmberg. Hoboken: J. Wiley & Sons.

Hyde, S. T., M. O'Keeffe and D. M. Proserpio. 2008. A short history of an elusive yet ubiquitous structure in chemistry, materials and mathematics. *Angew Chemie Int Ed Engl* 47: 7996–8000.

Israelachvili, J. N and S. Marcelja and R. G. Horn. 1980. Physical principles of membrane organization, *Quart Rev Biophys* 13: 121–200.

Israelachvili, J. and J. Wolfe. 1980. The membrane geometry of the prolamellar body. *Protoplasma* 100:315–321.

K. Larsson, K. Fontell and N. Krog. Chem. Phys. Lipids 27 (1980) 321.

Lam, H., D.-C. Oh, F. Cava, C. N. Takacs, J. Clardy, M. A. de Pedro, and M. K. Waldor. 2009. D-Amino acids govern stationary phase cell wall remodeling in bacteria. *Science*. 325:1552–1555.

Landh, T. 1995. From entangled membranes to eclectic morphologies: Cubic membranes as subcellular space organizers. *FEBS Lett* 369: 13–17.

Lane, N. J. and J. B. Harrison. 1979. An unusual cell surface modification: a double plasma membrane. *J Cell Biol* 39: 353.

Larsson, K. and R. P. Rand. 1973. Detection of changes in the environment of hydrocarbon chains by Raman spectroscopy and its application to lipid–protein systems. *Biochim Biophys Acta* 326: 245–255.

Larsson, K. and S. Andersson. 1986. A phase transition model of cooperative phenomena in membranes. *Acta Chem Scand* B40: 1–5.

Larsson K. 1989. Cubic lipid–water phases. Structures and biomembrane aspects. *J Phys Chem* 93: 7304–7314.

Larsson, M., O. Terasaki, and K. Larsson. 2003. A solid state transition in the tetragonal lipid bilayer structure at the lung alveolar surface. *Solid State Sci* 5: 109–114.

Lee, H., Y.-C. Cheng, and G. R. Fleming. 2007. Coherence dynamics in photosynthesis: protein protection of excitonic coherence. *Science* 316: 1462–1465.

Lehn, J.-M. 1995. *Supramolecular chemistry: concepts and perspectives*. Wiley-VCH, Weinheim.

Liang, H. and L. Mahadevan. 2011. Growth, geometry and mechanics of a blooming lily. *PNAS* 108: 5516–5521.

Livolant, F. 1991. Ordered phases of DNA in vivo and in vitro. *Physica A* 176: 117–137.

Luzzati, V. and F. Husson. 1962. The structure of the liquid-crystalline phases of lipid–water systems. *J Cell Biol* 12: 207–219.

Luzzati. V. and P. A. Spegt. 1967. Polymorphism of lipids. *Nature* 215: 701.

Luzzati, V. 1997. Biological significance of lipid polymorphism: the cubic phases. *Curr Opin Struct Biol* 7: 661–668.

McCollom, T. M. 2003. Formation of meteorite hydrocarbons from thermal decomposition of siderite (FeCO3). *Geochim Cosmochim Acta* 67: 311–317.

McCollom, T. M., B. Sherwood Lollar, G. Lacrampe-Couloume, and J. S. Seewald. 2010. The influence of carbon source on abiotic organic synthesis and carbon isotope fractionation under hydrothermal conditions. *Geochim Cosmochim Acta* 74: 2717–2740.

Medawar, P. B. 1967. A biological retrospect. In *The art of the soluble*. London: Methuen and Co. Ltd. (Originally published in 1965. *Nature* 207: 1327.

Michielsen, K. and D. Stavenga, D. 2008. Gyroid cuticular structures in butterfly wing scales: biological photonic crystals. *J R Soc Interface* 5: 85–94.

Morris R. B. 1975. Iridescence from diffraction structures in the wing scales of Callophrys rubi, the Green Hairstreak. *J Entomol A* 49: 149–154.

Nath, Utpal, Brian C. W. Crawford, Rosemary Carpenter and Enrico Coen. 2003. Genetic Control of Surface Curvature. *Science* 299: 1404–1407.

Needham. J. 1932. *Archeion 14: 509.* In A. Brown and A. L. Mackay, 2005. *J Biosci* 30: 407.

Noh, H., S. F., V. Liew, R. O. Saranathan, S. G. J. Prum, E. R. Mochrie, Dufresne, and H. Cao. 2010. How non-iridescent colors are generated by quasi-ordered structures of bird feathers. *Adv Mat* 22: 10.1002/adma.201090094.

O'Leary, M. H. 1981. Carbon isotope fractionation in plants. *Phytochem*. 20: 553–567.

Onslow, H. 1923. On a periodic structure in many insect scales, and the cause of their iridescent colours. *Phil Trans R Soc Lond B* 211: 1–74.

Open University Lecture 2009. Available at: <http://www.open.edu/openlearn/nature-environment/natural-history/ou-lecture-2009-download-the-discussion>.

Pearson L. T. and S. I. Chan. 1987. Pair distribution functions of cytochrome coxidase in lipid bilayers: evidence for a lipid-mediated repulsion between protein particles. *Chem Scr* 27B: 203–9.

RCSB Protein Data Bank. Available at: <http://www.rcsb.org/pdb/home>.

Robinson, C. 1956. Liquid-crystalline structures in solutions of a polypeptide. *Trans. Faraday Soc* 52: 571–592.

Saranathan, V., C. O. Osuji, S. G. J. Mochrie, H. Noh, S. Narayanan, A. Sandy, E. R. Dufresne, and R. O. Prum. 2010. Structure, function, and self-assembly of single network gyroid (I4132) photonic crystals in butterfly wing scales. *PNAS* 107: 11676–11681.

Savin, S., N. A. Kurpios, A. E. Shyer, P. Florescu, H. Liang, L. Mahadevan, and C. J. Tabin. 2011. *Nature* 476:57–62.

Schoen, A. H. 2012. Reflections concerning triply-periodic minimal surfaces. Interface Focus. doi:10.1098/rsfs.2012.0023.

Schröder-Turk, G. E., S. Wickham, H. Averdunk, F. Brink, J. D. Fitz Gerald, L. Poladian, M. C. J. Large and S. T. Hyde. 2011. The chiral structure of porous chitin within the wing-scales of Callophrys rubi. *J Struct Biol* 174: 290–295.

Senechal, M. 2012. *I died for beauty: a biography of Dorothy Wrinch*. Oxford: Oxford University Press.

Sharon, E., B. Roman and H. L. Swinney. 2007. Geometrically driven wrinkling observed in free plastic sheets and leaves. *Phys. Rev. E 046211*.

Simons, K. and G. van Meer. 1988. *Biochemistry* 27: 6197–6202.

Simons, K. and E. Ikonen. 1997. Functional rafts in cell membranes. *Nature* 387: 569–572.

Singer S. J. and G. L. Nicolson 1972. The fluid mosaic model of the structure of cell membranes. *Science* 175:720–31.

Sluckin, T. J., D. A. Dunmor, and H. Stegemayer eds. 2004. *Crystals that flow: classic papers from the history of liquid crystals*. CRC Press.

Thompson, D'Arcy Wentworth. 1942. *On growth and form*. Cambridge: Cambridge University Press.

Wiener, M. C. 2004. A pedestrian guide to membrane protein crystallization. *Methods* 34:364–372.

Wilts, B. D., K. Michielsen, H. De Raedt, and D. G. Stavenga. 2011. Hemispherical Brillouin zone imaging of a diamond-type biological photonic crystal. *J R Soc Interface* rsif20110730.

Zurek, W. H. 2009. Quantum Darwinism. *Nature Physics* 5: 181–188.

Notes on contributor

After studies at the University of Western Australia and Monash University, Stephen Hyde obtained a PhD in Physics at Monash University in 1986. His research career was kick-started as a research assistant with Professor Sten Andersson in Lund, where ideas on the relevance of curved surfaces to material structures, both inorganic and organic, were being developed by Sten. Since then he has spent most of his research career at the Department of Applied Mathematics, in the Research School of Physics at the Australian National University. His principal interest remains the exploration of topologically complex two-dimensional forms and their relevance to the natural world.

Correspondence to: Stephen Hyde, Email: stephen.hyde@anu.edu.au