

The Types: A Persistent Structuralist Challenge to Darwinian Pan-Selectionism

Michael J. Denton^{1,2*}

¹Aditya Jyot Eye Hospital, Mumbai, INDIA

²Discovery Institute, Seattle, Washington, USA

Abstract

Here I first review the structuralist or typological world view of pre-1859 biology, and the concept that the basic forms of the natural world—the Types—are immanent in nature, and determined by a set of special natural biological laws, the so called 'laws of form'. I show that this conception was not based, as Darwinists often claim, on a priori philosophical belief in Platonic concepts, but rather upon the empirical finding that a vast amount of biological complexity, including the deep homologies which define the taxa of the natural system, appears to be of an abstract, non-adaptive nature that is sometimes of a strikingly numerical and geometric character. In addition, these Types exhibit an extraordinary robustness and stability, having in many instances remained invariant in diverse lineages for hundreds of millions of years. Second, I show that neither Darwinism nor any subsequent functionalist theory has ever provided a convincing adaptive or functionalist explanation for the Types or deep homologies. Third, I discuss how recent advances have provided new support for the structuralist notion that the basic forms of life are immanent in nature. These include the discovery of the cosmic fine-tuning of the laws of nature for life as it exists on earth, and advances in areas of molecular and cellular biology, where it is apparent that a considerable amount of biological complexity is clearly determined by the self-organizing properties of particular categories of matter, rather than being specified in detail in a genetic blueprint as functionalism demands.

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* Email: mikedenton30@yahoo.com.au

INTRODUCTION

For two centuries biologists have been divided into two opposing camps, the so-called structuralist (or formalist) and functionalist schools of thought, regarding the fundamental nature of organic form [1; 2: chs. 4 and 5; 3]. The boxed quotes on page 2 illustrate the long-standing nature of this debate. According to the structuralist paradigm, a significant fraction of the order of life is the result of basic physical constraints arising out of the fundamental properties of matter—more specifically biological matter. These constraints limit the way organisms are built to a few basic designs; these include the deep homologies, for example the pentadactyl limb, and the basic body plans of the major phyla. The recurring patterns and persistence of these designs implies that many of life's basic forms arise in the same way as that of other natural forms such as crystals or atoms—from the self-organization of matter—and are thus *genuine universals*. Structuralists adhere therefore to a strictly “non-selectionist, non-historicist” view of the biological world.

Leading 20th-century structuralists include the inventor of the term ‘genetics,’ William Bateson [2: p. 409; 4], D’Arcy Wentworth Thompson, author of the classic structuralist work *On Growth and Form* [5], Rupert Riedl [6], Stuart Kauffman [7], Brian Goodman [8], and Stuart Newman [9; 10].

Although Gould was, as he himself confesses, a convinced pan-selectionist in his early years [2: p. 41], he was increasingly sympathetic to structuralism in his later years. In *The Structure of Evolutionary Theory* he writes: “I don’t see how anyone could read, from Goethe and Geoffroy down through Severtzov, Remane and Riedl, without developing some appreciation for the plausibility, or at least the sheer intellectual power, of morphological explanations outside the domain of Darwinian functionalism” [2: p. 43; 11: pp. 24–25].

According to the opposing paradigm, often referred to as functionalism, the main designs of life (pentadactyl limb, body plans, etc.) are not the result of physical law, that is, not

Structuralism vs. Functionalism: Then and Now

It is generally acknowledged that all organic beings have been formed on two general laws—Unity of Type and the Conditions of Existence. By unity of type is meant that fundamental agreement in structure, which we see in organic beings of the same class, and which is quite independent of their habits of life.

Charles Darwin, *Origin of Species* [1: p. 166]

These two principles have always dwelled together in exquisite tension. Any complete account of morphology must call upon both phenomena, for most organisms are well adapted to their immediate environment [conditions of existence], but also built on anatomical ground plans that transcend any particular circumstance. Yet the two principles seem opposed in a curious sense,—for why should structures adapted for particular ends root their basic structure in homologies that do not now express any common function (as in Darwin's example of mammalian forelimbs)? The designation of one principle or the other as the causal foundation of biology virtually defines the position of any scientist towards the organic world and its causes of order ... Shall we regard the plan of high-level taxonomic order as primary, with local adaptation viewed as minor wrinkles (often confusing) upon an abstract majesty? Or do the local adaptations build the entire system from the bottom up? This dichotomy set the major debate of pre-Darwinian biology ... [and] continues to define a major issue in modern evolutionary debates: does functional adaptation or structural constraint maintain priority in setting evolutionary pathways and directions?

Stephen J. Gould, *The Structure of Evolutionary Theory* [2: p. 252]

immanent in nature or arising from intrinsic physical constraints inherent in biological matter, but rather the result of specific adaptations built additively by selection during the course of evolution, to serve particular functional ends, ends that are imposed by the environment and that are external to the organism itself. Adaptations built in this way are contingent, in the sense that they are *undetermined by natural law*. On this functionalist view, organisms are in essence like machines, complexes of functional parts arranged to serve particular adaptive ends. This is of course the currently prevailing, mainstream view. All Darwinists, and hence the great majority of evolutionary biologists, are functionalist by definition, because according to Darwinism *all* evolution is the result of adaptation to meet environmental contingencies. In this essay I will critique Darwinian functionalism and defend the structuralist alternative.

PRE-DARWINIAN STRUCTURALISM

The discovery that the living world is organized into an ascending hierarchy of ever more inclusive classes, each defined by a particular unique homology or suite of homologies of an apparently abstract nature, was one of the major achievements of pre-Darwinian biology [3: ch. 2; 12; 13: ch. 1]. Although the causal foundation of this remarkable hierarchy was unknown (and still is today), it was widely assumed in the early 19th century that it was an immanent feature of nature and part of the eternal order of the world. As Mary Winsor points out, just as Newton had provided a causal explanation for the regularities in the motions of the planets described by Kepler, so it was expected that biology would eventually have its Newton who would provide a scientific explanation for the hierarchic pattern of nature. She comments, “Many biologists seemed to feel that although their field was not yet as exact, coherent and logical as Newtonian science, it had the potential of becoming so ... The role of a scientist was to discover within the

confusing diversity of living things the underlying order and lawfulness” [13: p. 175].

The idea that life on earth is the result of a lawful natural process was explicitly affirmed by Richard Owen in the concluding chapter of his *Anatomy of Vertebrates*. He claimed that the path of evolution was “preordained ... due to an innate tendency ... by which nomogenously created [generated by law] protozoa have risen to the higher forms” [14: vol. 3, p. 809]. Owen was not exceptional in this regard. As Dov Ospovat points out in his *Development of Darwin's Theory* [13: p. 20] William Carpenter, one of Owen's contemporaries, believed “that the *laws* that define the plan of creation were ... impressed on matter in the beginning [to bring about] ... the creation and succession of life.” Russell shows in his classic *Form and Function* that nearly every pre-Darwinian biologist, including such luminaries as Karl Ernst von Baer, Etienne Geoffroy St. Hilaire, Henri Milne-Edwards, E. Serres, J.F. Meckel, Carl Gustave Carus, H.G. Bron, Theodore Schwann, and many biologists after Darwin, particularly on the continent (such as Ernst Haeckel) believed life's overall order to be the result of *lawful*, if unidentified, processes [2: pp. 1070–71; 15: p. 241]. The concept that life's hierarchic pattern is inherently lawful was also witnessed in the attempt of early 19th-century taxonomists to organize classification schemes in terms of geometric and numeric patterns, such as the quinary system of William Sharp Macleay and Swainson [12: ch 4; 3: pp. 45–47]. Even Huxley was attracted to these orderly circular systems. His remark, “The circular system appears to me to stand in the same relation to the true theory of animal form as Kepler's Laws to the fundamental doctrine of astronomy” [12: p. 91], serves to underline further that the core aim of early 19th-century biology was to find lawful explanations of the biological realm. Mary Winsor comments regarding Huxley [12: p. 91], “He had not found the answer, biology's law of gravity, but he was searching in that direction.” However anomalous it may seem in the context

of today's biology, profoundly wedded as it is to functionalist notions and the concept of life's forms as ultimately contingent (see below), the belief that the order of life is immanent in the fabric of things was the very *Zeitgeist* of early 19th-century biology [12; 13].

The notion of a lawful biology, where all the major types are part of the world order no less than inorganic forms, naturally lent itself to teleological speculation. This is nowhere more apparent than in the views of Louis Agassiz, who saw the Types as ideas in the mind of God [2: ch. 4], and saw the whole taxonomic system as part of God's grand plan of creation. In his *Essay on Classification* he states, "To me it appears indisputable, that this order ... [is] in truth but translations into human language of the thoughts of the Creator" [16: p. 9]. Owen also saw nature's order as the result of a Divine plan. He even goes as far in his *Vertebrate Anatomy* to claim "the horse to have been predestined and prepared for man" [14: vol. 3, p. 796].

Homologous 'numerology'

Owen famously termed the homologies 'primal patterns' in his great classic *On the Nature of Limbs*. In Owen's words, homology expressed "the essential character of a part which belongs to it in its relationship to a predetermined pattern, answering to the idea of the Archetypical World in the Platonic cosmogony, which archetype or primal pattern is the basis supporting all the modifications of such a part" [17: pp. 2–3]. Owen's somewhat flamboyant phraseology should not be taken to imply, however, that Owen himself, or the majority of early 19th-century biologists, viewed the Types as anything other than lawful immanent features of nature [3; 12; 13; 18], analogous to atoms or crystals or any other set of natural forms (see below on the metaphor of the crystal). As mentioned above, Owen himself talks of "nomogenously created protozoa," and in the last sentence of *On the Nature of Limbs* [17] he refers to the "natural laws" responsible for vertebrate evolution.

The claim of pre-Darwinian structuralism that the homologous patterns (and the entire grand hierarchic system) are immanent features of the changeless order of nature was not based on an a priori adherence to Aristotelian or Platonic theories of nature [3; 12]. On the contrary, the structuralist position was supported by two fundamental observations: that the homologies appeared to be *non-adaptive abstract patterns*, and that in some cases they appear to have remained *invariant for hundreds of millions of years* in diverse lineages.

In chapter fourteen of the *Origin*, Darwin describes a number of homologous patterns, including the well-known pentadactyl limb, and concedes, "What can be more curious than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should all be constructed on the same pattern, and should include similar bones, in the same relative positions?" (see Figure 1) [1: p. 382]. That such homologous patterns based on the number five have no apparent specific adaptive utility in any living organism was admitted by Darwin. He comments in the *Origin* in a key passage, "Nothing can be more hopeless than to attempt to explain this similarity of pattern of members

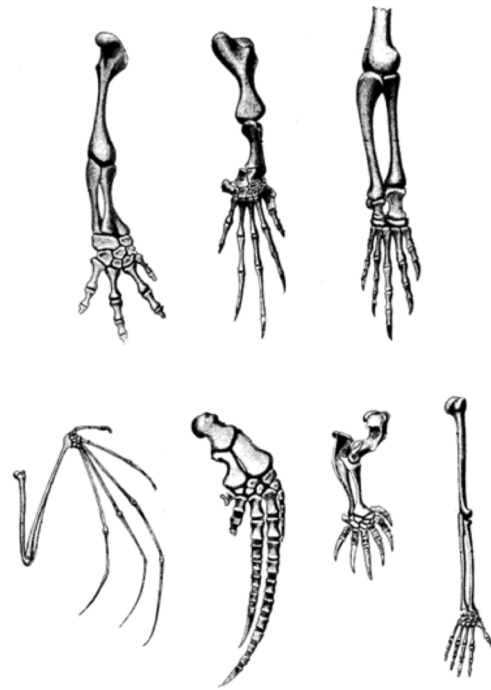


Figure 1: The pentadactyl limb, showing the structure of the forelimbs of various vertebrate species. Upper row, left to right, salamander, toad, crocodile; lower row, bat, whale, mole, human. The digits are displayed with digit one (the thumb in man), the most anterior digit, to the right. Although in some species the number of digits is reduced, no terrestrial vertebrate has more than five true digits. The salamander has four, having lost digit five [19]. The mole has a pseudo-digit, as has the panda, derived in both cases from modified carpal bones and positioned anterior of digit one (to the right in the figure). Modified from an original image by Wilhelm Leche (1909) in *Man, Origin, and Evolution*, and now in the public domain. doi:10.5048/BIO-C.2013.3.f1

of the same class, *by utility* or by the doctrine of final causes. The hopelessness of the attempt has been *expressly admitted by Owen* in his most interesting work *On the Nature of Limbs*." [1: p. 383] [emphasis added]. And nothing emphasizes the "hopelessness" more obviously than the curious numeric and geometric aspects of so many homologous patterns.

Consider the 'numerology' of the insect body plan. The insect body is divided into three parts: head, thorax, and abdomen. The thorax consists of three segments and each bears a pair of legs, six altogether. Eleven segments can be recognized in the abdomen of most juvenile insects and although some insect adults—including Coleoptera (beetles) and Hymenoptera (wasps, bees, ants, etc.)—have less than eleven, no insect has more than eleven. The legs of all insects consist of no more than five components, namely the coxa, the trochanter, the femur, the tibia, and the tarsus; the tarsus itself is typically divided into five subsegments (see Figure 2). The insect mouth in all the many diverse species always consists of four parts from front

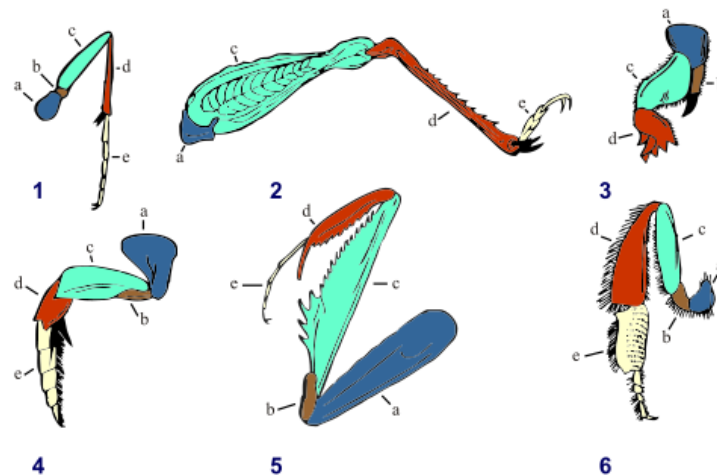


Figure 2: The insect limb. All insect limbs consist of no more than five basic parts: a. coxa; b. trochanter; c. femur; d. tibia; e. tarsus. As can be seen in the figure, different insects have limbs adapted for many different functions: 1. cursorial legs are modified for running (ground beetle); 2. saltatorial hind legs are adapted for jumping (locust); 3. fossorial forelegs are modified for digging (mole cricket); 4. natorial legs are modified for swimming (diving beetle); 5. raptorial forelegs are modified for grasping and catching prey (mantis); and 6. the worker bee (honeybee) leg is modified for pollen collection. (Image from http://en.wikipedia.org/wiki/Insect_morphology, and used under the Creative Commons CC0 1.0 universal public domain dedication.) doi:10.5048/BIO-C.2013.3.f2

to back—the labrum, the mandibles, the maxillae, and the labium. And all insects possess two antennae, which are mobile jointed appendages [20].

Homologous ‘numerology’ is not limited to the insects or the pentadactyl limb. In the case of the cephalopods, for example, the Octopoda (octopuses) have eight tentacles, while the Teuthoidea (squids) have ten, two of which are considerably longer than the other eight [21: ch. 10, p. 485]. Again, octopuses and squids have two gills, while other cephalopods including *Nautilus* have four. The echinoderms (starfishes and sand dollars) exhibit a pentamerous symmetry [21: ch. 14]. Among the Cnidaria (jellyfishes, sea anemones and corals) there are a great variety of intriguing radial symmetries. Among the Scyphozoa (jellyfishes), most exhibit a tetramerous symmetry [21: p. 116], “having their parts symmetrically repeated round their oral aboral axis to the number 4 or multiples of 4 ... [however, some species] are built on a plan of six, and have a hexamerous symmetry.” Among the Anthozoa (sea anemones and related polypoid forms), different classes are differentiated by different types of radial symmetries and can be classified on number and arrangement of tentacles and mesenteries and number and arrangement of septa [21: p. 125]. One colonial subclass (Alcyonaria) possesses eight pinnate tentacles forming a marginal circle on the oral disc and eight mesenteries attached to the gullet [21: p. 125]: “The eight symmetrically arranged tentacles and mesenteries give the polyp what seems to be an octamerous radial symmetry.” Another subclass, the Zoantharia, are subdivided into a variety of groups exhibiting complex six-fold symmetries with “mesenteries in cycles of 6, 12, or multiples of 6” [21: p. 130]. The textbooks of invertebrate zoology are full of innumerable additional examples.

The basic divisions within the vertebrates are also defined by

homologous patterns that are no less numeric than in the invertebrates. We have already referred to the pentadactyl limb of the tetrapods. Among mammals, the number of cervical vertebra is seven in nearly all placental orders, including species as diverse as the giraffe, the mouse, the whale, the elephant, and man [14: vol. 3]. Most placental mammalian orders have no more than 44 teeth and these are subdivided into molars, pre-molars (possessing cusps), canines, and incisors (only the Cetacea depart markedly from this formula) [14: vol. 3]. Again, in all placental mammals the cerebral cortex is divided into six layers of cells or laminations [22: p. 544].

Geometry and numerology also pervade the botanical realm. All higher angiosperm flowers (eudicots) conform to a remarkable pattern of concentric whorls [23] consisting of four nested whorls: an outermost whorl of sepals, surrounding a whorl of petals, which in turn surround a ring of stamens and in the center a small circular region containing the pistil [24; 25]. Although some of the earliest angiosperms depart from this classic pattern, having their floral organs arranged in spiral formations instead of whorls [23; 26], *a spiral is no less abstract than a whorl!*

Invariance

In addition to their remarkable abstract character, the other striking feature of the homologies is their great stability through millions of generations and in diverse phylogenetic lines. The pentadactyl limb, for example (see Figure 1), first emerged some 400 million years ago and has remained essentially invariant in all tetrapod lines ever since [27: ch. 6]. Some tetrapods have less than five digits [19] but no tetrapod has more than five true digits. Where there is an additional digit this is, as in the case of the mole [17: Fig. 2] or panda [28: p. 22] never a

true digit and invariably co-opted from material derived from elsewhere, such as the carpal bones [27: ch. 6]. Pentadactyly appears to be an absolute constraint. The ‘concentric whorl plan’ of the Angiosperm flower has remained unchanged at least in the higher eudicot clade for 100 million years, since the late Cretaceous. The defining features of insects and even of the various insect subgroups such as the ants have also remained constant for millions of generations [29]. The abstract nature and deep invariance of the homologies and the Types is a fact, a simple straightforward biological fact. However remarkable it might be—and it is certainly very remarkable, in Darwin’s own words “curious” and “striking” [1: pp. 382–383]—it was in the early 19th century and it is still today *a fact based on observation*.

Adaptive masks

Despite their focus on the apparently abstract homologous patterns, neither Owen nor any of the other pre-Darwinian typologists denied the fact of adaptation or its significance [2: p. 324]. However, they saw adaptation to be a secondary, peripheral phenomenon, the result not of natural law (order from within), but of a response to environmental conditions (imposing an external order from without). Owen [17: p. 41] coined the elegant descriptive term ‘adaptive masks’ to highlight their superficial and secondary nature compared with the underlying ‘predetermined’ or ‘primal patterns’ [17: pp. 2–3], upon which they were crafted to serve various adaptive functions. Owen saw the primal patterns to be generated during development by what he called the ‘polarizing force,’ while the adaptive masks were the result of another fundamental mechanism he termed the ‘adaptive force’ [18: xxix; 30: ch. 4].

Russell points out that Haeckel, for example, distinguished between “the internal *Bildungstrieb* [formative force] ... the mechanical effect of the material structure of the crystal or the germ, and adaptation, or the external *Bildungstrieb*, [defined as] modifications induced by the environment” [15: p. 248]. Environmental adaptation was also seen by H.G. Bron as one of the major causal factors shaping organic form [15: p. 203].

Goethe’s view was similar. Goethe asserted the primacy of formal patterns, but conceded the vital if secondary role of adaptation, saying, for example, “We can best see this in a species of seal whose exterior has taken on a great deal of fish character [adaptive form] while its skeleton [formal structure] still represents the perfect quadruped.” Commenting on Goethe’s view, Gould writes, “Internal formation acts as the primary source that ‘must find external conditions.’ Adaptation may then shape a range of diversity from an underlying form, but the archetypal pattern cannot be explained by these secondary modifications, and the adaptations themselves can only express a superficial restructuring of inherent order” [2: pp. 289–290].

It is important to stress that structuralism therefore implies that organic order is a *mixture of two completely different types of order, generated by two different causal mechanisms*: a primal order generated by natural law, and a secondary adaptive order imposed by environmental constraints (by natural selection according to Darwinists, by Lamarckian mechanisms and by intelligent design according to current design theorists). The

adaptive order of living things represents a completely different sort of order, outside of the explanatory framework of structuralism altogether. This means that structuralism per se can never give a complete causal explanation for all organic order. Structuralism is *not* a biological theory of everything.

Metaphor of the crystal

Given the lawful *Zeitgeist* of pre-Darwinian biology and given the enigmatic *abstract nature* of the homologies and their *invariance* in so many diverse kinds of organisms and through such vast periods of time, it was a small inferential step to view them as changeless natural forms analogous to crystals or atoms. Geoffroy, perhaps the leading continental formalist, assumed the homologies to have “powers” analogous to atoms and other unalterable elements of the physical world [15: p. 78]. Owen also used the crystal analogy unambiguously in the final chapter of his *Anatomy of Vertebrates*, in the context of a discussion of the causes of segmentation: “The repetition of similar segments in a vertebral column and of similar elements in a vertebral segment, is analogous to the repetition of similar crystals” [14: p. 789]. The metaphor was also used by Theodore Schwann, the co-founder of the cell theory. In the last chapter of his *Microscopical Researches* he draws extensive parallels between cells and crystals [31: pp. 212–213]:

The process of crystallization in inorganic nature ... is ... the nearest analogue to the formation of cells ... Should we not therefore be justified in putting forward the proposition that the formation of the elementary parts of organisms is nothing but a crystallization, and the organism nothing but an aggregate of such crystals? ... If a number of crystals capable of imbibition are formed, they must combine according to certain laws so as to form a systematic whole, similar to an organism.

The metaphor was used extensively by Haeckel who, echoing Schwann, talks of “cells as organic crystals, of crystal trees, of the analogy between assimilation by the cell and the growth of crystals in a mother liquid” [15: p. 248].

The fact that many different crystal forms can be generated from a small number of basic patterns added to the attraction of the analogy. In the case of calcite, for example, the rules permit the construction of about 600 different molecular arrangements which can be combined to build over 2000 different combinations [32: pp. 78–79]. If the homologies are lawful aspects of the world order, no less than atoms or crystals, then just as for atoms or crystals, there should exist a set of laws, “Laws of Biological Form” [33: pp. 4–10; 34; 35], which would provide a rational and lawful account of the diversity of organic forms, analogous to the laws of chemistry or the laws of crystallography, which account rationally for the diversity of chemical compounds and crystals, and which allow for a rational deductive derivation of all possible chemical compounds or crystals. Typical of the search for these elusive laws was the attempt of C.G. Carus, H.G. Bronn and E. Haeckel to develop what

Russell [15: p. 33] terms “a ‘theoretical’ morphology of living things, after the fashion of the morphology of crystals with their sixteen possible types.”

Although the term ‘self-organization’ was not current in the 19th century, it was implicit in the typological belief that organic forms belong to a special class of natural forms, analogous to atoms and crystals, which *do* arise from the self-organizing properties of matter. The parallel between pre-Darwinian typology and the current interest in self-organizational processes was discussed recently by Fodor and Piattelli-Palmarini [36: ch. 5], and by Depew and Weber [37: p. 483], who comment, “[the current] self-organizational conception represents a renewal in the age of molecular biology ... of the long displaced but extremely powerful Geoffroyian [pre-Darwinian typological] research tradition.” The pre-Darwinian types might also be described as ‘basins of attraction’ in the current terminology of dynamic systems theorists [7: chs. 12 and 13; 38].

Essentialism story¹

The current widespread impression is that pre-Darwinian structuralists derived their belief that the deep homologous patterns were changeless natural forms or types from all sorts of discredited metaphysical beliefs. This impression has been severely critiqued by recent researchers, and has been shown to be largely a myth created by 20th-century advocates of the neo-Darwinian evolutionary synthesis, what Amundson calls Synthesis Historiography [3: p. 11]. As Amundson shows, whatever their metaphysical leaning, the concept of *the type as a basic natural form* was not derived primarily from any a priori metaphysical belief, but from solid empirical observations. He comments [3: p. 18], “We will fret over their metaphysics no more than we fret over Kepler’s ... They do not deserve the disdain to which they have so long been subject.” The structuralist conception of life, and especially of an ascending hierarchy of taxa of ever widening comprehensiveness as an immanent feature of nature, was close to the classic Aristotelian world view [39: pp. 94–95], but it was based on the *facts*, not on a philosophical a priori.

From crystal to watch

The “Laws of Form” biology of the pre-Darwinian era, with its emphasis on evolution by natural law and its conception of a rational order underlying the diversity of life, represented a grand scientific vision, whose heroic goal was nothing less than the unification of biology and physics. It collapsed primarily because it failed to identify the elusive causal ‘Laws of Form’ which might have provided a rational causal account of organic form [3: ch. 4, pp. 99–102]. It failed to explain how the evolution of the basic types, from cell forms to the body plans of the major phyla, or the deep homologies such as the pentadactyl limb, might have been generated by natural law. Owen, for

example, had no idea what the polarizing force actually was, nor Haeckel the *Bildungstrieb* (formative force). That they had no convincing lawful explanation for the grand homologies was explicitly conceded by Owen in the final paragraph of *On the Nature of Limbs* [17]: “To what natural laws or secondary causes the succession and progression of such organic phenomena may have been committed we as yet are ignorant.”

THE DARWINIAN REVOLUTION

The failure to find laws of form that could account for the basic forms of the biological world and explain the course of evolution opened the door for Darwin and ushered in the functionalist revolution. After 1859, the structuralist conception of the basic order of the biological realm as a product of natural law was overthrown, and the pre-Darwinian concept of organisms as real natural existents, as necessary parts of the world order, like atoms or crystals, was abandoned. As was pointed out in a previous paper [35: pp. 328–329]:

Instead a new model of organic form—that of the machine or artifact—took its place. Necessity was replaced by contingency and natural law was replaced by natural selection. Organic forms were now viewed as contingent mutable assemblages of matter, like the constructs of a child’s erector set, put together during the course of evolution piece by piece by natural selection.

The adoption of the ‘contingent mutable artifact’ as the metaphor of organic form ushered in the modern era of biology and changed the whole explanatory framework of biological science, from what was a structuralist/functionalist framework (primal abstract patterns by law, adaptive masks by environmental selection), to a purely functionalist conception of nature. The very naturalness of life—the idea of life as a necessary part of nature—was abandoned. *The metaphor of the crystal was replaced by that of the watch.*

This notion implicit in the functionalist view of life that came to dominate biology after Darwin, namely that organisms are ultimately artifactual beings analogous to machines (i.e., no more than complex functional or adaptive assemblages of parts like a watch [40]), long predated the Darwinian revolution. In the 17th century, Descartes claimed in his *Treatise on Man* that the human body was a complex machine whose functions “follow naturally ... entirely from the dispositions of the organs ... [no more nor less] than do the movements of a clock or other automaton, from the arrangement of its counterweights and wheels” [41: p. 113]. (See also his *Discourse on Method* and *Principles of Philosophy*.) English natural theology also adopted the mechanistic analogy, as witnessed by Ray’s *The Wisdom of God as Manifest in the Works of Creation* [42], and Paley’s *Evidences* [40]. That Darwin himself saw organisms to be nothing more than complex functional mechanical assemblages—bundles of adaptations built up bit by bit to satisfy a series of historical environmental challenges—is clear in this well-known passage from his book on the fertilization of orchids:

¹ Essentialism is the idea that reality consists of a set of essentially distinct forms, each characterized by the possession of a set of unique attributes. Thus all the members of different categories, such as men, women, plants, cats, dogs, and so forth, share the same essential defining characteristics or traits; there is no continuum or intermediate series of forms between them. Thus the forms differ fundamentally. Applied to the biological realm, essentialism implies that the biological types are a distinct and changeless set of basic forms.

If a man were to make a machine for some special purpose, but were to use old wheels, springs, and pulleys, only slightly altered, the whole machine, with all its parts, might be said to be specially contrived for its present purpose. Thus throughout nature almost every part of each living being has probably served in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct forms [43: pp. 283–284].

Modern-day hard Darwinists have stuck to the machine analogy, as is obvious on any reading of George Williams, Jacques Monod, Richard Dawkins, or Daniel Dennett.

Functional legitimations

If functionalism is to provide a comprehensive explanatory framework of *all* biological order, it must be capable of accounting plausibly not only for adaptive complexity but also for the apparently non-adaptive order of the organic realm, including the universe of apparently non-functional homologies that underlie the whole natural system.² Darwin's explanation for such non-functional homologies is that they represent 'left-overs' of evolution, ancient adaptations no longer useful but incorporated into the genetic system and passed down through the generations.³ Darwin gave this explanation for persistent pattern with no apparent adaptive utility in many places in the *Origin of Species*:

The chief part of the organization of every living creature is due to inheritance, and consequently though each being is well fitted for its place in nature, many structures have now *no very close and direct relation to present habits of life*. We cannot believe that the similar bones in the arm of a monkey, in the fore-leg of the horse, in the wing of a bat, and in the flipper of the seal, are of special use to these organisms. *We may safely attribute these structures to inheritance* [1: p. 160] [emphasis added].

If we suppose that an early progenitor—the archetype as it may be called—of all mammals, birds, and reptiles, had its limbs constructed on the existing general pattern, for *whatever purpose they served*, we can at once perceive the plain signification of the homologous construction of the limbs throughout the class [1: p. 383] [emphasis added].

Clearly Darwin's 'explanation' is more a case of special pleading than an 'explanation.' On the one hand he admits with

² Whether Darwinism can give an account of the adaptive complexity of living things in terms of incremental adaptive steps is controversial, and rejected not only by supporters of intelligent design [44–46], but by many non-ID supporters among mainstream biologists, including Günter Wagner [47], Richard Prum [48], Scott Gilbert (<http://www.suzanmazur.com/?p=4>), and Stuart Newman (<http://www.archaeology.org/online/interviews/newman.html>).

³ Note that Darwin was also aware that some non-adaptive order might be what Gould refers to as spandrels [2: ch. 11]. Darwin concedes that "if man goes on selecting, and thus augmenting, any peculiarity, he will almost certainly modify unintentionally other parts of the structure, owing to the mysterious laws of correlation" [1: p. 9].

Owen that the homologies serve no adaptive purpose in living forms, but is prepared to speculate that they did once serve some purpose in ancestral forms. Nowhere in *On the Origin Of Species* does he attempt to provide any significant justification for this radical claim, by showing, for example, that five fingers were adaptive in the ancestral tetrapod, or that the three thoracic segments were adaptive in the ancestral insect. Given their numeric and geometric character, to show that the homologies were *once upon a time* adaptive poses a Herculean challenge to the functionalist framework.

Consider the origin of the pentadactyl pattern. To provide a strictly functionalist explanation of the origin of this pattern, Darwin would have had to give an adaptive explanation for each element of the pattern, in other words, to explain why five digits were preferred over four or six, or why two distal bones were preferred over one or three or four, and one proximal bone over two or three. In the end he had no explanation. There is still no detailed supportive scenario today, showing how these particular arrangements were adaptive in the ancestral species.

Moreover, the forelimbs and hind limbs are based on the same homologous pattern. Why should incremental selection pressures on a forelimb and hind limb—that are different in every limbed species—have miraculously generated the same functional form in both the hind limb and forelimb in the ancestral species? Similar problems are faced in accounting for the specific adaptive significance of *all* the universe of homologous patterns in nature [4]. But even if we could somehow account for the origin of such strikingly numeric patterns in adaptive terms we would then be faced with the additional and far more difficult problem of explaining how selection for function could have *conserved the pattern for millions of generations after it ceased to have any adaptive significance*.

Consider this. To accept Darwin's legitimation we must assume that a fin—more specifically the arrangement of bones in a fish fin—underwent gradual adaptive change supervised by selection so that bit by bit the pattern approached and finally resulted in the pentadactyl pattern. While this process is at least conceivable (at least in the case of either the forelimb or hind limb), the next phase, which would involve the freezing of the pentadactyl pattern, is highly problematical. We have to believe that a *variable adaptive form* became an *invariant, non-adaptive form* at a particular instant in evolutionary time and was conserved through all the subsequent generations and phylogenetic lines in both fore and hind limbs.

Of course the challenge to functionalism is not restricted to providing an adaptive explanation for the pentadactyl pattern of the vertebrate limb. The same challenge is present in all attempts to explain the other homologous patterns, such as the numerology of the insect body plan or the concentric ring pattern of the angiosperm flower.

The ubiquity of non-adaptive pattern

A particularly difficult challenge to Darwinian and functionalist assumptions (which is as pertinent today as it was in 1859) is the existence of a vast universe of non-adaptive forms and patterns in nature which no biologist, not even the most

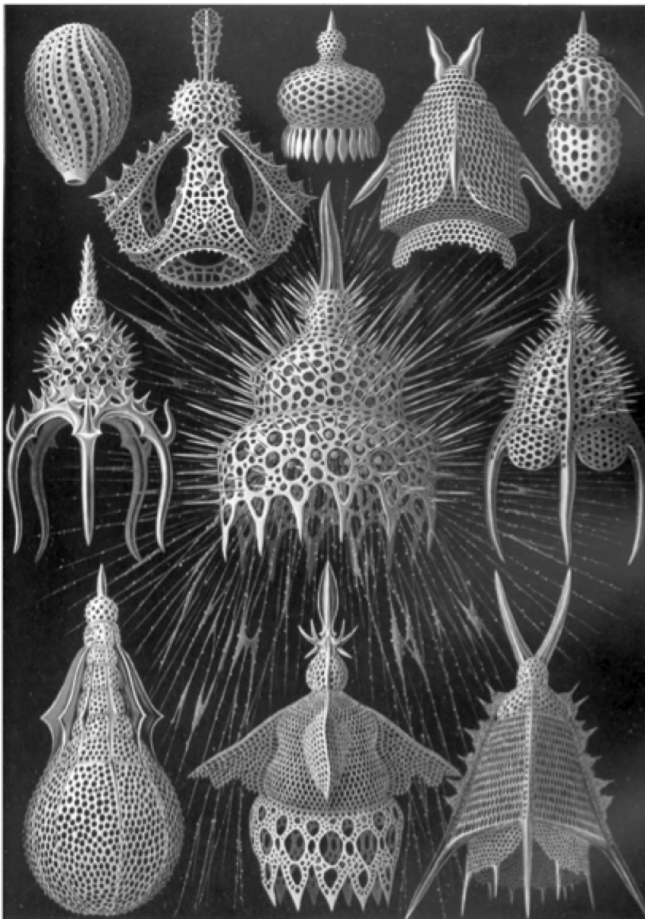


Figure 3: Radiolarian shells. Abstract pattern is not restricted in nature to the deep homologies, but is ubiquitous throughout the living realm. Plate 31 from Ernst Haeckel's *Kunstformen der Natur* (Artforms of Nature), 1904. doi:10.5048/BIO-C.2013.3.f3

convinced functionalist or Darwinist, has ever claimed to serve specific adaptive functions.⁴ This raises an obvious problem—on what *objective* grounds can the homologous patterns like the pentadactyl limb be differentiated from the host of patterns that no one doubts are non-functional?

To take one example, the shells and tests of unicellular organisms, including radiolaria, foraminifera, and diatoms, display a bewildering universe of diverse forms, some highly geometric but others as abstract as a Kandinsky painting (see Figure 3). That many of these forms are abstract structures produced by the direct action of physical law, no less than the generally round shape of a cell, was wonderfully argued in D'Arcy Thompson's *On Growth and Form* [5: p. 873]: "The forces that bring about

the sphere, the cylinder or the ellipsoid are the same yesterday and tomorrow. A snow crystal is the same today as when the first snows fell. The physical forces which mold the forms of *Orbulina*, of *Astrorhiza*, of *Lagena* or of *Nodosaria* today were still the same, and for aught we have reason to believe the physical conditions under which they worked were not appreciably different, in that yesterday we call the Cretaceous." Gould concurs, as he comments, "These forms [radiolarian and foraminiferan tests] are ... no more ... subject to specific accounts of historical filiation than are the varied shapes of snow flakes or quartz crystals" [2: p. 1206].

It is not just in the unicellular world that nature abounds in what appear to be abstract formal patterns. Even the most cursory and passing observation of some of the most familiar of natural forms, such as the forms of leaves and many other botanical patterns, or the variety of phyllotactic⁵ arrangements that might be observed in any suburban garden, leads to the conclusion that a vast amount of biological order serves no specific adaptive end.

In the context of what appears to be a veritable universe of non-adaptive form permeating all nature, the Darwinian assumption that the grand homologies once were adaptive in ancestral forms is self-evidently ad hoc. Put simply, neither Darwin nor any subsequent Darwinist has ever provided cogent reasons for accepting the grand claim that *all* complexity in biology (including all currently non-adaptive forms) has resulted from past adaptive and purposeful shaping of structures to serve functional ends.

Although neither Darwin, nor any subsequent Darwinist, has provided any convincing functionalist explanation of the deep homologies that unite each of the main taxa, nonetheless, since Darwin, biology has been tightly wedded a priori to a functionalist/adaptational conception of living nature, avoiding the challenging possibility that much of the order of nature might be fundamentally non-adaptive and thus beyond functionalist explanations, *even in principle*. In short, the grand fact of what appears to be a veritable universe of non-adaptive order is the nemesis, the Achilles heel, of the whole functionalist tradition. Accept the reality of formal, non-functional patterns as one of the *primary facts of biology*, and Darwinism becomes a special theory explaining or attempting to explain adaptation, but nothing more.

The genetic blueprint

An inevitable consequence of adopting the functionalist paradigm, and the notion that organic forms are ultimately contingent mechanical assemblages of matter [machines], is the need to postulate a genetic blueprint in the genes (analogous to the blueprint which specifies a machine) that specifies in detail the mature form. This is because contingent order, unlike natural form, cannot arise spontaneously as the result of natural law or from the self-organization of matter. If the types are indeed (as structuralists insist) natural forms like crystals, there is no

⁴ See W. Bateson, *Materials for the Study of Variation* [4]. Bateson, who coined the term 'genetics' and was the founder of the *Journal of Genetics*, vigorously opposed throughout his life the externalist and functionalist view of organic form. But again, like Owen's, Bateson's worldview was based on a mountain of empirical evidence that a non-adaptive substratum of order does indeed permeate the biological realm. In his *Materials for the Study of Variation*, he documents many examples of non-adaptive variation in nature, especially between closely related species. He pointed to the way in which various countable structures in living things (such as the number of vertebral segments in various groups of vertebrates, or the number of joints in insect limbs) varied between species and argued that the pattern of variation arises from internal, non-adaptive forces within the organism itself and is not the result of external forces such as selection for function.

⁵ Phyllotactic patterns are the arrangements of leaves on a plant stem, scales on a cone axis, or florets in a composite flower head. Many are spiral arrangements that exhibit intriguing mathematical relationships.

need to specify in detail the higher order of the organic system in a detailed blueprint, because, as in the case of a crystal or any other natural form, ‘nature’ takes the basic components (atoms, molecules, categories of biological matter) and organizes them into their native forms. Functionalism demands preformism (a detailed blueprint specifying the final form), while structuralism implies epigenesis (emergent form based on self-organizational principles apart from any blueprint).

The modern version of the blueprint model was first formulated clearly by August Weismann [49], who was a convinced functionalist and mechanist. For him an organism was no more than a complex bundle of adaptations, and this complex of adaptations was a purely contingent mechanical arrangement of matter, which in his words, “could have been other than it is” [49: vol. 2, p. 307]. The structuralist view, “that species are vital crystals,” he rejected.⁶

Weismann envisaged the germ plasm to contain a set of genetic blueprints, analogous to the blueprints that specify the design of a machine. He called them ‘determinants’ [49: vol. 1, p. 335], each of which specified a specific feature or trait of the adult phenotype in a highly deterministic, unidirectional way. Linde-Medina points out:

This [gene-centric] conceptualization of development makes the search for organizing principles a fruitless enterprise. If form is encoded in the genes, it is essentially arbitrary, and biological order is contingent. In this case, evolutionary biology becomes essentially a historical narrative and any regularity across taxa would be interpreted, not as evidence for the existence of natural laws—as it is the case in other sciences—but as historical contingencies now recorded in genes. [50]

Precisely because mechanism logically necessitates preformism, it is no coincidence that nearly all the founders of the mid-20th-century molecular biological revolution, including Monod [51], Crick [52], and Watson [53], were strong mechanists *and* preformists like Weismann, and fervently committed to the blueprint model. Given the logical necessity for blueprints to account for the transmission of *contingent* order through time, and given the adherence of modern biology to mechanism, it is little wonder the search for the blueprints in the genes, which would justify mechanism and the functionalist/Darwinian paradigm, became the holy grail of 20th-century biology [54: p. 6].

As a logical necessity of the functionalist-Darwinian framework, the blueprint provides a means of validating the paradigm: if one can show that a particular organic form—a

cell type, a body plan or any other deep homology—is specified in a genetic blueprint, then functionalism in that particular instance is vindicated.

Summary

Although functionalism came to govern biology after 1859 (especially in the English-speaking world) primarily because the structuralists failed to identify the laws of form which might explain the Types in non-functionalist terms, the persistent failure of functionalism to provide plausible explanations for the non-adaptive patterns of nature *at any time* during the past 150 years may well turn out to be a decisive factor predisposing 21st-century biology to re-examine sympathetically the Typological and structuralist claim—that physics plays a significant role in the generation of organic form. Indeed I believe that this primal failure mandates a sympathetic rethinking of the whole pre-Darwinian and structuralist worldview.

NEW SUPPORT FOR THE LAWS OF FORM

Despite the great difficulty in reducing non-adaptive patterns to functionalist explanations, structuralism has been largely sidelined in the English-speaking world since the Darwinian revolution. But it has refused to die. As cited above, a succession of first-rate biologists have continued to argue that physical law plays a significant role in the determination of organic form. Moreover, during the 20th century several advances in different fields have provided new support for the pre-Darwinian idea of life and its deep structures as immanent in the world order.

The fitness of the laws of nature for life

The first clear evidence that at least some key features and characteristics of life on earth are determined by natural law, or more specifically by the properties of matter, came to light in the late 19th and early 20th century as a result of advances in organic chemistry, biochemistry, and physiology. This new evidence, which implied that life’s basic chemical and physiological design was determined by natural law, was assessed and presented by Wallace in his *The World of Life*, published in 1910, and a few years later by Lawrence Henderson in his great classic *The Fitness of the Environment*, published in 1913 [55]. In *The Fitness*, Henderson argued that carbon-based life as it exists on earth depends critically on what is in all likelihood a unique, mutual, synergistic fitness among the properties of the carbon atom, organic compounds, water, carbon dioxide, and oxygen, that enables them to assemble the complex chemical systems we associate with life. In other words, the basic design of life is immanent in the properties of matter and not an artifact of time and chance, as Darwinism implies. This idea is discussed in depth in my recent article in *Bio-Complexity* [56] and in *Nature’s Destiny* [57].

Further evidence that the laws of nature may be fine-tuned for life on earth came from advances in 20th-century physics and astronomy, which revealed that if the various fundamental forces and constants that determine the structure of the cosmos and the properties of its constituents did not have precisely the values they do, there would be no stars, no supernovae, no

⁶ In Volume 2 of *Evolution Theory*, Weismann writes, “[To some authors] the species appears, so to speak, as a vital crystallization ... [or] as an equilibrium of living matter, which becomes displaced from time to time, and passes over into a new state of equilibrium.... The species is thus something conditioned from within ... just like a crystal.... But it seems clear to me that the species is not a life-crystal in the sense that it must, like a rock-crystal, take form in a particular way.... The species is essentially a complex of adaptations, of modern adaptations which have been recently acquired, and of inherited adaptations which have been handed down from long ago—a complex which might well have been other than it is, and indeed must have been different if it had originated under the influence of other conditions of life” [49: vol. 2, p. 307].

planets, no atoms, no life. This fine-tuning is so delicately balanced that it gives the striking impression that basic laws of physics have been specifically designed to generate a cosmos specifically adapted for life as it exists on earth [55–60]. As Paul Davies summarizes:

The numerical values that nature has assigned to the fundamental constants, such as the charge on the electron, the mass of the proton, and the Newtonian gravitational constant, may be mysterious, but they are crucially relevant to the structure of the universe that we perceive. As more and more physical systems, from nuclei to galaxies, have become better understood, scientists have begun to realize that many characteristics of these systems are remarkably sensitive to the precise values of the fundamental constants. Had nature opted for a slightly different set of numbers, the world would be a very different place. Probably we would not be here to see it [58: preface, vii].

Fred Hoyle famously commented on the fine-tuning necessary to generate carbon and the higher elements in the stars, “A common sense interpretation of the facts suggests that a super intellect has monkeyed with physics, as well as chemistry and biology, and that there are no blind forces worth speaking about in nature” [58: p. 118].

Might Hoyle be right in thinking that the fine-tuning of the universe extends to the laws of chemistry and biology? If the laws of nature are, for whatever reason, fine-tuned to generate environmental conditions ideally suited to the forms of life that exist on earth, so fine-tuned that, as Davies confesses, “The impression of design is overwhelming” [61: p. 203], it is surely not so outrageous to envisage that the laws of nature might be also biologically fine-tuned to generate the grand hierarchy of forms themselves. In short, the discovery that the cosmos is fine-tuned for life’s environment provides powerful circumstantial support for the laws of form and the notion that life’s basic designs are immanent in the world order. The extrapolation is intriguing and very hard to resist. It is particularly hard to resist when one considers that the fitness of the cosmic, chemical and physiological environment for life on earth extends even to organisms like ourselves [55; 57]. Such an extrapolation would bring us very close to the 19th-century conception of life as immanent in the world order, and with the notion that the main taxa are invariant universals, analogous to atoms or crystals determined by laws of form.

Laws of molecular form

The notion that the some of the basic forms of life on earth might be lawful intrinsic elements of the world order has already found support at least at the molecular and cellular level. Ironically the very icon of modern biology, the double helix itself, is a natural form determined in all its exquisite geometry by the laws of chemistry. Both its double helical structure and its chemical stability that confer upon it such a wonderful fitness for its genetic role [57: ch. 7] are determined by the laws of

chemistry. It may perform one of the most important of biological *functions*, and its base sequence may contain ‘complex specified information’ [45; 46], but its basic structure arises from the self-organizing properties of matter. Perhaps no entity in biology exemplifies so beautifully Owen’s two types of order: the helix as the ‘primal pattern,’ and the base sequence as the ‘adaptive mask’!

Proteins. Protein folds represent one of the most remarkable cases where a set of physical rules determine the forms of an important class of complex molecular structures [35; 62; 63]. Intriguingly, the rules that generate the thousand-plus known protein folds have now been largely elucidated and remarkably they amount to a set of ‘laws of form’ of precisely the kind sought after by early 19th-century biologists (see above). These rules arise from higher-order packing constraints of alpha helices and beta sheets, and constrain possible protein forms to a small number of a few thousand structures [64]. In conformity with pre-Darwinian structuralism, the protein forms are analogous to a set of crystals [35]! And while all proteins exhibit adaptive modifications, these are in perfect conformity with pre-Darwinian structuralism, clearly what Owen (see above) would have termed ‘adaptive masks,’ built upon an underlying invariant form or ‘primal pattern.’ Thus the globin fold, for example, has been adapted in hemoglobin to carry oxygen (Owen’s adaptive mask), but the underlying form (the primal pattern) is essentially an abstract pattern determined by physical law, one of the permissible protein forms constructed out of alpha helices as determined by the rules of protein folding.

Moreover as Daniel Weinreich [65] has shown, even the adaptations built upon the folds are greatly constrained by biophysical properties and the structures of the folds themselves. He concludes, “It now appears that intramolecular interactions render many mutational trajectories selectively inaccessible, which implies that replaying the protein tape of life might be surprisingly repetitive” [65]. This is a sentiment that would be shared by Owen and most of his contemporary 19th-century typologists.

Lipids. During the 1960s, the structure of another important self-organizing biological structure was elucidated: the bilayer lipid membrane that forms the outer boundary of all living cells [66]. The same basic membrane structure (the primal pattern) makes up the endoplasmic reticulum, and encloses the nucleus, the mitochondrion, the chloroplast and so forth. Lipid membranes form a vast variety of tubes and vesicles, and various types of sheets. This diversity was described by Waddington:

[Closed membrane surfaces] may assume a large variety of different forms but one can perhaps consider them as variants on three basic types: the vesicle, the disc, and the tube ... The tube ... [may be considered] a vesicle in which one dimension is very much elongated ... the majority of subcellular organelles are built up as complexes of vesicles, diderms [two skinned vesicles], and tubes ... Golgi bodies for instance consist essentially of a pile of flattened vesicles ... Mitochondria again are complex closed vesicles constructed out of a double membrane

[67: pp. 105–107].

That these bio-lipid forms arise mainly from the self-organization of the membranes themselves, by energy minimization without any direction from anything like a genetic blueprint, is evidenced by the fact that many analogous forms can be generated *in vitro* in solutions of amphiphilic compounds. Some dramatic examples of the self-organizing capabilities of inorganic solutions of amphiphiles are given by Ball [68; 69: ch. 2]. As the concentration of amphiphiles in an aqueous medium increases, eventually micelles form; as more surfactant is added, plane lamellae form; eventually, as the concentration of the lipid is increased even more, a bicontinuous phase is formed consisting of a vast labyrinth of interconnected tubes.⁷

In living systems these basic lipid forms (primal patterns), like the protein folds, are modified to serve specific adaptive ends (adaptive masks). Edelman and Denton describe how it happens [70]:

Different lipids and proteins can bend and distort the basic membrane form [the primal pattern] into various globular forms, vesicular forms or tubules [adaptive masks] [71] ... As Huttner and Schmidt [71] comment: “The shape of biological membranes reflects the shape of their principle constituents—that is membrane lipids and integral membrane proteins” ... And reporting some fascinating work on a membrane altering protein dynamin they remark: “Dynamin alone is sufficient to change the shape of liposomes, causing either tubulation or vesiculation depending on lipid composition.” Thus by changing the lipid and protein constituents of membranes the cell is able to generate vesicles from planar surfaces; tubules from planar surfaces and vesicles from tubules. Like the zoo of 3D protein folds, none of these lipid forms is specified in any detail in the DNA. All spontaneously emerge by self-organization from particular categories of matter in a process analogous to a phase transition.

Although each specific lipid form, like the lamellae of the chloroplast or the outer segment of the photoreceptor, is adapted to serve some particular function (photosynthesis in the case of the chloroplast, phototransduction in the case of the photoreceptor outer segments), and each represents an ‘adaptive mask,’ there is no doubt that the underlying form—layered stacks of bilayer lipid membranes—is primarily determined by purely physical law.

Microtubules. The microtubular aster is another example of a molecular form that clearly arises directly out of the intrinsic self-organizing properties of its basic constituents. The aster is generated by spontaneous interactions between microtubules and molecular motors, i.e., from “the intrinsic characteristics of its parts” [72]. During its formation, as described by Kirschner and Mitchison [73], the developing spindle appears to be searching for a pre-ordained natural energy minimum. It

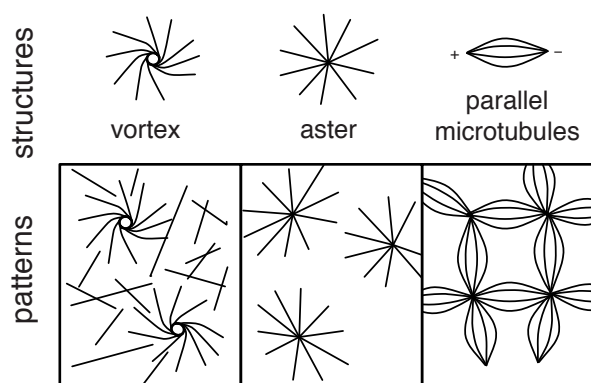


Figure 4: Microtubular Forms. Shown are various self-organizing patterns produced *in vitro* or *in silico* by mixtures of microtubules and motors. When motors having various physical properties cross-link microtubules (lines) and move along them by hydrolyzing ATP, they can produce various steady-state structures. Vortices and asters are produced when only one [type] of motor is present; parallel microtubules connected at their tips can be produced when plus end and minus end motors are mixed with microtubules. (Redrawn with minor changes from [75, figure 4], with permission from Maney Publishing (<http://maneypublishing.com/index.php/journals/isr> and <http://www.ingentaconnect.com/content/maney/isr>). doi:10.5048/BIO-C.2013.3.f4

‘finds’ this minimum via a seeming ‘infinity’ of different routes, not a precisely specified assembly pathway, as occurs in the case of phage.

The aster is only one of several well-defined, self-organized microtubular forms, several of which may be generated *in vitro* [74] or *in silico* [75], merely by changing the basic constituents that are present (see Figure 4). A vast variety of complex structures can be generated by modifying the molecular environment in which microtubules self-organize, including the very complex adaptive microtubular structures that play such a crucial role in determining the forms and functions of cells [76]. It should also be noted that actin and myosin molecules can self-organize *in vitro* into a variety of forms as well, including ring structures [77]. Thus microtubules, actin, and myosin are all capable of self-assembly *in vitro* into structures resembling those in cells, in a manner analogous to the lipid forms mentioned above [69: ch. 2].

All the self-organized molecular biological structures cited above—DNA, protein folds, membrane forms, microtubular forms, actin and myosin forms—arise from the self-organizing, intrinsic, physical and chemical properties of their constituents. Although their constituents are specified in the genes, in no case is the three-dimensional, assembled structure specified by a genetic program. Rather, in every case the primary natural self-organizing propensity of a particular category of matter is exploited and secondarily modified to serve some adaptive end.

Cell form

Although the ontological status of cells is still not clear, there is a growing consensus among cell biologists that the form of cells arises mainly from the self-organization of their constituents rather than by instruction from a detailed blueprint in the genome as functionalism/mechanism demands [77; 78: p. 336;

⁷ See also the Wikipedia article on lyotropic liquid crystals at: http://en.wikipedia.org/wiki/Lyotropic_liquid_crystal.

79–81]. Karsenti comments that despite the attraction of the blueprint model there are no “simple linear chains of causal events that link genes to phenotypes” [77: p. 255]. And wherever there is no simple linear causal chain linking genes with phenotypes, wherever self-organization intervenes between genes and phenotype—at any level in the organic hierarchy, from cells to body plans—the resulting form is bound to be to a degree epigenetic and emergent, and cannot be inferred from even the most exhaustive analysis of the genes.

Moreover, envisaging how a blueprint could *actually* determine the spatial deployment of the cell’s constituents has always seemed problematical [82: p. 50]. Waddington commented, “If, for instance, actin and myosin do not, on account of their own inherent properties, unite together in a particular way ... how can any gene provide instructions that they shall be united in that manner?” [67: p. 119]. Researchers in supramolecular chemistry and nanotechnology, striving to fabricate complex molecular structures in the mesoscopic realm, have recently echoed Waddington’s doubts, pointing out that there are formidable, perhaps insurmountable, theoretical barriers to mechanical, bottom-up microfabrication in this domain [83; 84]. One of the few alternatives to bottom-up fabrication is to exploit the principle of self-organization, as a means of deploying matter into complex ordered structures in the mesoscopic realm of the cell. Clearly, physical law necessarily plays a much more significant role in determining the order of life at a cellular level than is generally assumed in functionalist circles.

The role of physical forces in shaping global cell form was defended by D’Arcy Thompson in his magisterial *On Growth and Form* [5: vol. 1, chs. 4 and 5], an epitome of 20th-century structuralist and typological thought. In the opening paragraph of chapter 4, Thompson makes his commitment to structuralism unambiguous, citing an earlier 19th-century author who considered cells to be analogous to atoms and who looked forward to a “science of organic [cell] forms.” The same structuralist theme—the idea that physical law plays a determinative role in shaping the universe of cell forms was explored more recently by Stuart Kauffman, who talks of cells in the terminology of complexity theory, referring to them as representing a set of ‘basins of attraction’ [7: chs. 12 and 13].

Intriguingly several commentators have recently invoked Thompson’s *On Growth and Form* [5], foreshadowing a move back towards structuralist thinking in cell biology [7; 76; 85]. The editor of a series of recent papers on cell form in *Current Biology* commented, “With the current renaissance (or *naissance*) of physical thought in cell biology, Thompson’s book might be moving along from the apocryphal towards the canonical” [85: R743]. And Eric Karsenti, one of the leaders of the self-organization revolution in cell biology, recently commented:

The principles that are associated with self-organization processes [in the cell] tend to indicate that the driving force behind the diversity of life and its evolution is not mainly selection. Instead, it may derive largely from *the intrinsic properties of living matter ...* In a sense we are moving back to the views of D’Arcy

Thompson, who thought that biologists overemphasize the role of evolution [functionalism] over that of physical laws in the origin of growth and form [emphasis added] [77].

To this author’s knowledge, to date the form of no individual cell has been shown to be specified in detail in a genomic blueprint. As mentioned above, between genes and mature cell form there is a *complex hierarchy of self-organization and emergent phenomena*, rendering cell form *profoundly epigenetic*.

Organismal form

The past three decades have witnessed a spectacular increase in knowledge of the genetic and developmental mechanisms underlying the generation of organismal form. These advances have led to the new science of evo-devo (evolutionary developmental biology) and are properly described by one of the leading researchers in the area, Sean Carroll, as ‘revolutionary’ [86]. They have provided massive new insights into the development of such classic homologies as the pentadactyl limb [87; 88], angiosperm flowers [24; 25], and the insect and vertebrate body plan [86; 89]. One fascinating aspect of these advances has been the discovery that a limited set of genes and developmental mechanisms (for example, Hox proteins, signaling proteins like Sonic Hedgehog, chemical gradients, etc., or what Carroll has termed the ‘toolkit’ [86: ch. 1, Fig. 3.7]), are involved in the generation of all the types, body plans, deep homologies, etc., and indeed of all higher organismic forms. The discovery that all organisms utilize the same limited ‘toolkit of genes and developmental mechanisms’ undoubtedly has very significant evolutionary implications—suggesting, for example, that development constrains the paths of evolutionary change (a topic of much recent discussion in evo-devo circles)—but it provides no profound new insights into the ultimate ontological status of the types and deep homologies, that is, whether they are immanent in nature (as structuralism implies) or ancient contingent adaptations, “randomness caught on the wing” as Jacques Monod expressed it in *Chance and Necessity* [51: p. 98].

In short, the existence of the toolkit does not imply that there are blueprints in the genes specifying in exacting detail the forms of organisms. The fundamental reason for this is that organic form at all levels of the biological hierarchy, not just at the cellular level (see Karsenti’s remarks above), is essentially *emergent and epigenetic*, arising from complex dynamic self-organizing mechanisms during development. This is now widely acknowledged by researchers in many different fields [2; 7; 8; 10; 90–95].

The Pentadactyl Limb. For a dramatic illustration of the failure of gene-centric explanations of the homologies, despite the ‘toolkit revolution,’ one need look no further than the pentadactyl plan of the tetrapod limb. Twenty years ago, the expectation was high that the Types would finally be explained in terms of the gene blueprint model, thus vindicating the functionalist and Darwinian interpretation of the Types as ancient adaptations (contingent assemblages of matter) deeply embedded in the developmental genetic system, and propagated down through the generations. In 1992 Colin Tabin proposed a

simple model referred to as the Hox code [27: ch. 6; 96], which envisaged that the pentadactyl digital pattern resulted from the fact that there were only five Hox genes expressed across the developing autopod, with a specific Hox gene for each of the five digits. But subsequent work showed that this was simplistic and the mechanisms responsible for generating the five digits are far more complex, involving higher-order dynamic interactions between various developmental processes.

A decade after the Tabin paper, as new evidence accumulated, the Hox code was seen to be untenable. As Hinchliffe commented [96]:

Molecular theories of tetrapod digit specification have been put forward as in the ‘one domain = one digit’ Tabin (1992) hypothesis. This was based on the finding of a nested set of Hox D expression domains across the antero-posterior axis of the digital plate in chick and mouse limb buds. All Hox D 11–13 genes were expressed posteriorly but only D 11 anteriorly, corresponding with posterior and anterior digits respectively. But later, more evidence was obtained showing that the posterior pattern spread into the anterior plate, and such an oversimple ‘one gene domain, one structure’ theory became untenable ... Instead Hox D 11–13 appears to correlate with a general digit formation capacity of the digital plate.

Although the mechanism that limits tetrapods to five digits is still not understood, the most recent work suggests that a Turing-type reaction-diffusion model plays a critical role in generating the digits. Intriguingly, in a 2010 Stuart Newman paper, the researchers were able to simulate many vertebrate limb patterns in computer simulations of reaction-diffusion models [87]. And in the most recent paper in the field, Sheth et al. [88] confirmed the Newman model. In it the authors comment:

The formation of repetitive structures (such as stripes) in nature is often consistent with a reaction-diffusion mechanism, or Turing model, of self-organizing systems. We used mouse genetics to analyze how digit patterning (an iterative digit/nondigit pattern) is generated ... Combined with computer modelling, our results argue for a Turing-type mechanism underlying digit patterning, in which the dose of distal Hox genes modulates the digit period or wavelength [88].

It is surely a profound irony not only that the simplistic gene-centric Hox code is outmoded, a representative of a dated gene-centric/gene-deterministic paradigm, but also that its current successor involves a reaction-diffusion mechanism considered by structuralists for decades as a classic mechanism for the generation of unexpected and unpredicted emergent patterns arising spontaneously from simple, physical, self-organizational mechanisms. Brian Goodwin, one of the most ardent defenders of the structuralist paradigm in the late 20th century, devoted chapter 3 in his book *How the Leopard Changed its Spots* [8] to describe the various fascinating patterns that can be

generated by these mechanisms, and eulogized about them as classic cases of emergent, surprising, self-organized patterns *not specified in the genome*. One can hardly imagine a model more diametrically opposed to the gene-centric, reductionist, Hox-code model than the notion that digit number and identity are generated as the result of a reaction-diffusion mechanism.

It turns out that twenty years after the Hox code and the era of hard gene-centricity the questions ‘why pentadactyly?’ and ‘why no more than five digits?’ remain quite inexplicable in terms of the functionalist framework. To date, everything currently known about the development of the autopod is consistent with a structuralist interpretation of the pentadactyl pattern as a robust, natural, emergent form. (Admittedly, much is still to be learned about limb development before a *definitive* verdict in favor of structuralism can be delivered.)

The pentadactyl limb is not unique—the same argument applies to the insect body plan. Despite evo-devo, despite the toolkit, no one can provide a functionalist/gene-centric explanation for why there are no more than eleven abdominal segments, or no more than the five basic divisions of the insect limb, or what the fundamental constraints driving these patterns are. No answer to such fundamental questions exists within a functionalist framework, as is obvious on any reading of the latest evidence with regard to insect development in any major text (for example [97: ch. 9]). Indeed, *in every case* (to the author’s knowledge), bottom-up genetic explanations fail to account for homologous patterns, thus presenting a major challenge to the entire functionalist project, and by default providing powerful support for the alternative structuralist view—that these patterns are *self-organizing emergent forms arising spontaneously from the properties of particular categories of biological matter*.

Robustness. These same advances in developmental genetics have revealed that the homologies are even more robust⁸ than previously believed. For example, in many species there is massive underlying genetic and developmental variance in the way the toolkit is used, despite employing the same basic elements (Hox proteins etc.) to generate the homologies [47; 98; 99]. This observation is highly consistent with the structuralist paradigm, strongly suggesting that these patterns are indeed immanent in nature.

The fact that regenerated organs are, as Amundson recently pointed out, “clearly homologous to those originally developed in embryos, but ... constructed in a different manner and aris[ing] from different tissue sources,” has always been seen as evidence of the robustness of the organismal pattern [3: p. 241]. Hans Driesch cites many examples [33] in his *The Science and Philosophy of the Organism*; he saw the phenomenon as indicative of a vital force which he called the *entelechy*. Some examples are indeed truly remarkable. In the case of the newt, for example, virtually every organ in the body can be regenerated after

⁸ Robustness is the capacity of a complex system or whole to maintain a constant configuration in the face of contingent perturbations in its lower-level constituents. For example, the ability of an organism to maintain the same phenotype in the face of genetic mutations is termed mutational robustness.

surgical excision in the adult organism [100].

But the observation that is the most supportive of the structuralist claim that homologies are emergent, robust, self-organizing *natural forms*, is the fact that *the same homologous structure may arise in different ways, involving different genes and genetic pathways in different species* [98; 99]. To take a classic example, the early embryos of all vertebrates are very similar at the post-gastrula stage when the vertebrate body plan is first apparent, but the developmental processes and pathways that lead to this homologous stage differ markedly in different classes.

As another case, consider insect segmentation. One might have imagined that the underlying developmental genetic mechanisms that so stringently conserve the body plan would have been themselves stringently conserved—an assumption that would lend itself to a gene-centric/functionalist account. But in fact, three different mechanisms are utilized to generate segments, even among closely related species within one insect order (among beetles, for example). Although the segmentation pattern of all adult insects is the same—three thoracic segments, and no more than eleven abdominal segments [20]—three different developmental mechanisms are used to generate segments in different species [98], the so called short germ-band, intermediate germ-band, and long germ-band. In long germ-band development, the entire anterior-posterior segmentation pattern is determined simultaneously in the embryo [97: ch. 9], while in short germ-band development the segments are generated by successive temporal subdivision of a posterior growth region. In the first case, a spatial sequence is formed *all at once*, whereas in the other a spatial sequence is *also a temporal sequence*. Liu and Kaufman [99] comment:

The insect body consists of a head of six or seven segments, a thorax of three, and an abdomen of eight to eleven segments, and is essentially invariant across species. Although it makes intuitive sense that differing developmental mechanisms should lead to differing final morphologies, the converse seems counter-intuitive; that differing developmental trajectories should arrive at the same endpoint. Yet this is the case with insect segmentation.

Curiously, the same radical switch between simultaneous specification and temporal specification also occurs in the case of the pentadactyl limb. While in most species the digital pattern emerges simultaneously, in certain species the digits are formed sequentially in a temporal succession from digit one to digit five [19]. So again the same pattern is derived in two radically different ways. Many other cases of extremely different generative means to the same end might be mentioned. For example, poly-embryos in parasitic wasps are a radical departure from the canonical embryogenesis followed in most wasp species [101: ch. 6]. In this case an individual fertilized egg divides multiple times, giving rise to a mass of undifferentiated cells (a polygerm), which then splits into clusters of cells, with each cluster forming an embryo that develops into a ‘normal wasp.’

Revelations of *the stability of homologies in the face of different*

generative processes in different species provide clear support for the notion that the homologies are robust natural kinds. As Günter Wagner, a leading authority in the field of evolutionary developmental biology, comments:

Developmental mechanisms and pathways have a tendency to shift under the continuing presence of the developmental types. The genetic machinery that produces segments in grasshoppers is in important ways different from that in a fruit fly. Genes which are essential for segmentation in fruit flies are not even expressed in grasshoppers, e.g., *even skipped* and *ftz*. [emphasis added] [47].⁹

It was always apparent that the adaptations built upon the homologies, Owen’s adaptive masks, like the various vertebrate limbs built upon the underlying pentadactyl pattern, are far more variable than the underlying homology itself. From the advances in developmental genetics it is now clear that, in many instances, the homologous patterns are *also* more robust than the underlying generative process and the gene circuits responsible for their assembly during development. This is truly remarkable. There is variation *above* (the various adaptive forms built upon the homology in different species) and variation *below* (the variable generative processes by which the homologous pattern is derived in development in different species), while the homologous pattern itself remains invariant across the many lineages in which it is conserved.

Acting like ‘strange attractors,’ the homologies appear to be exerting a mysterious determinate influence on the biological matter in which they form. Whatever the reason for their curious robustness, there is no doubt at present that, as Wagner admits, “[T]here is still *no explanation for the stability of the developmental type* ... [Giving an explanation is] the most urgent theoretical problem in the unification of development and evolution” [emphasis added] [47].

Structuralist Advocates.

One of the prominent advocates of the role of self-organization at all levels of the biological hierarchy is Stuart Kauffman, a self-confessed admirer and follower of D’Arcy Thompson [7: p. 644]. In his magisterial book *The Origins of Order*, he describes his work as an attempt to seek the origin of biological order in “the generic properties of complex systems”. This order he sees as “casting an image of underlying law over biology” [7: p. 644].

Another leading structuralist is Stuart Newman, a long-time advocate of physics as an important arbiter of organic form, who argues that the physical properties of cells and tissues impose constraints on the way they spontaneously associate to form higher-order complexes and patterns [10]. He has shown that the biophysical properties of clusters of cells are capable of generating all manner of complex structures and patterns, including the major patterns of gastrulation [104]. In other

⁹ In *Evolution: A Theory in Crisis* [102], I cited de Beer’s [103] monograph—*Homology: The Unsolved Problem*—to argue that homology is not explained by assuming that homologous structures are inherited from a common ancestor. Nearly three decades later I think de Beer’s comments, and the thrust of the chapter on homology in *Evolution: A Theory in Crisis*, have been entirely vindicated.

words, higher-order form arises from the intrinsic properties of special categories of biological matter. Basic physical processes, including cohesion, viscoelasticity, diffusion, spatiotemporal heterogeneity based on lateral inhibition, and multistable and oscillatory dynamics work together to:

... mold cell masses into only those morphologies which are characteristic of chemically and mechanically excitable mesoscopic materials, e.g., hollow, multilayered, elongated, segmented and branched forms. But these are, in fact, the common morphological motifs of all metazoan body plans and organ forms, both in the invertebrates and vertebrates, appearing repeatedly over the course of evolution despite there frequently being no common ancestor between organisms with the same feature. [104]

In a recent interview he comments, “You can actually predict the kinds of physical forces clusters of cells are susceptible to and calculate that those physical forces are sufficient to cause some of the clusters to be hollow, multilayered and segmented. Some of them will be elongated and some will have appendages.”¹⁰

Another researcher whose work on vertebrate embryology supports the structuralist agenda is physicist Vincent Fleury [105], who has shown that hydrodynamic processes are associated with and appear to drive much of the emerging form of the vertebrate embryo before and in the stages immediately following gastrulation. These involve a variety of self-organizing phenomena, some involving vortex-like cellular movements.

Christopher Cherniak’s work investigating the optimization of neural wiring also has structuralist implications [106–108]. Cherniak has shown [106] that in the case of the nematode, for example, the neural connections between its 302 neurons are optimized to minimize connection length. The actual layout turns out to be the best possible out of forty million alternatives. As he comments [106], “To current limits of accuracy ... the actual placement appears to be the best of all possible layouts; this constitutes strong evidence of perfect optimization.” The same principle appears to hold in the case of far more complex vertebrate nervous systems, where the optimization is way beyond discovery by Darwinian-type trial-and-error searches [106], suggesting that higher-order, organizational, structural principles may be involved. Indeed, as he comments, “The neural optimization paradigm is a structuralist position postulating innate abstract internal structure—as opposed to an empty slate account, without structure built into the hardware” [36: p. 81]. Fodor and Piattelli-Palmarini even go as far as to state that his research indicates “a pre-formatting” of nature for neuroanatomical optimization” [36: pp. 80–81], and entitle the chapter describing his work as ‘Return of the Laws of Form’ [36: ch. 5].

Radical epigenesis

If it is indeed the case that the properties of matter play an important role in the determination of organic form, then this implies that development is bound to be a *radically epigenetic process*. In other words, no matter how extensive the genetic

analysis of development is in decades to come, no matter how much information is in the genome, a complete explanation of development can never be given purely in terms of genetic blueprints in the DNA, or from even the most exhaustive analysis of the information in the egg cell. This is because causal factors *external to the genome*, residing in the self-organizing properties of special categories of biological matter, are critically involved in guiding the developmental process. If the claims of structuralism are valid, then this leads to the prediction: *No complete explanation of development will ever be given in terms of genetic blueprints or any version of the preformist doctrine.*

CONCLUSION

The primary structuralist premise that life’s basic forms are a natural and lawful part of the order of the world is a perfectly rational and naturalistic conception—every bit as rational, surely, as the post-Darwinian denial of life’s fundamental lawfulness and naturalness, and the post-1859 reassignment of organisms from the realm of nature to the realm of the artifact. Future researchers may well look back in astonishment at the post-Darwinian era in which most biologists deemed life’s forms mere artifacts of time and chance, with no less significance in the cosmic order than a wind-blown pattern of leaves.

Although no biologist can deny that adaptation is ubiquitous in the living world, *the Darwinian claim that ALL organic order, including the deep homologies, can be reduced to functionalist explanations is far from compelling.* After 150 years of focused functionalist effort, the grand taxonomic system and the ascending hierarchy of homologous patterns has still not been adequately accounted for in functionalist/adaptive/Darwinian terms.

The evidence presented in this review has highlighted the following observations: the profound *fitness of the laws of nature* for life as it exists on earth, revealed by advances in 20th-century cosmology, fundamental physics, and biochemistry; the failure to find the elusive genetic blueprints demanded of the functionalist paradigm; the revelation that at least some of the core molecular, cellular, and even higher organismic forms of life are the emergent result of the self-organization of matter; and the developmental robustness of the type, a robustness which recent advances have re-emphasized. When these observations are taken in conjunction with the ‘primal failure’ of the functionalist/adaptationist paradigm to explain the deep homologies and the existence of types, it is hard to refuse the possibility that the 21st century will witness a full-scale structuralist revival. Perhaps the metaphor of the crystal may yet eclipse the metaphor of the watch, and the grand taxonomic system return to its proper ontological status as an intrinsic part of the timeless order of nature.

¹⁰ <http://www.archaeology.org/online/interviews/newman.html>

1. Darwin C (1872) *On the Origin of Species*, 6th ed. Murray (London).
2. Gould SJ (2002) *The Structure of Evolutionary Theory*. Belknap Press of Harvard University Press (Cambridge, MA).
3. Amundson R (2007) *The Changing Role of the Embryo in Evolutionary Thought*. Cambridge University Press (Cambridge, UK).
4. Bateson W (1992) *Materials for the Study of Variation Treated with Especial Regard to Discontinuity in the Origin of Species*. Johns Hopkins University Press (Baltimore).
5. Thompson DW (1942) *On Growth and Form*. Cambridge University Press (Cambridge, UK).
6. Riedl R (1978) *Order in Living Organisms: A Systems Analysis of Evolution*. Wiley (Chichester).
7. Kauffman SA (1993) *The Origins of Order: Self-organization and Selection in Evolution*. Oxford University Press (New York).
8. Goodwin BC (2001) *How the Leopard Changed Its Spots: The Evolution of Complexity*. Princeton University Press (Princeton, NJ).
9. Newman SA (2002) Developmental mechanisms: Putting genes in their place. *J Biosci* 27:97–104.
10. Forgács G, Newman S (2005) *Biological Physics of the Developing Embryo*. Cambridge University Press (Cambridge, UK).
11. Allmon WD (2009) The Structure of Gould: Happenstance, Humanism, History and the Unity of His View of Life. In: Allmon WD, Kelley PH, Ross RM, eds. *Stephen Jay Gould: Reflections on His View of Life*. Oxford (New York), pp 3–68.
12. Winsor MP (1976) *Starfish Jellyfish and the Order of Life*. Yale University Press (New Haven).
13. Ospovat D (1995) The Development of Darwin's Theory: Natural History, Natural Theology, and Natural Selection, 1838–59. Cambridge University Press (Cambridge, UK).
14. Owen R (1866) *On the Anatomy of Vertebrates*. Longmans, Green and Co. (London).
15. Russell ES (1916) *Form and Function*. Murray (London).
16. Agassiz L (1859) *Essay on Classification*. Longman, Brown, Green; Longman and Roberts (London).
17. Owen R (1848) *On the Nature of Limbs*. John Van Voorst (London).
18. Amundson R (2007) Form versus Function. In: Amundson R, ed. *On the Nature of Limbs: A Discourse*. Chicago University Press (Chicago), pp xv–li.
19. Lamb T, Beamer DA (2012) Digits lost or gained? Evidence for pedal evolution in the dwarf salamander complex (Eurycea, Plethodontidae). *PLoS ONE* 7:e37544. doi:10.1371/journal.pone.0037544
20. Imms DA (1964) *A General Textbook of Entomology*. Methuen (London).
21. Shrock WH, Twenhofel WH (1953) *Principles of Invertebrate Paleontology*. McGraw-Hill (New York).
22. Nolte J (2009) *The Human Brain: An Introduction to its Functional Anatomy*. Mosby/Elsevier (Philadelphia, PA).
23. Soltis DE, Chanderbali AS, Kim S, Buzgo M, Soltis PS (2007) The ABC model and its applicability to basal angiosperms. *Ann Bot* 100:155–163. doi:10.1093/aob/mcm117
24. Coen ES, Meyerowitz EM (1991) The war of the whorls: Genetic interactions controlling flower development. *Nature* 353:31–37. doi:10.1038/353031a0
25. Weigel D (1995) The genetics of flower development: From floral induction to ovule morphogenesis. *Annu Rev Genet* 29:19–39. doi:10.1146/annurev.ge.29.120195.000315
26. Friis EM (2011) *Early Flowers and Angiosperm Evolution*. Cambridge University Press (Cambridge, UK).
27. Clack JA (2012) *Gaining ground: The origin and evolution of tetrapods*. Indiana University Press (Bloomington).
28. Gould SJ (1992) *The Panda's Thumb: More Reflections in Natural History*. Norton (New York).
29. Grimaldi D, Agosti D (2000) A formicine in New Jersey Cretaceous amber (Hymenoptera: formicidae) and early evolution of the ants. *P Natl Acad Sci USA* 97:13678–13683. doi:10.1073/pnas.240452097
30. Rupke N (1994) *Richard Owen: Victorian Naturalist*. Yale University Press (New Haven).
31. Schwann T (1847) *Microscopical Researches*. Sydenham Society (London).
32. Lima-de-Faria A (1988) *Evolution without Selection: Form and Function by Autoevolution*. Elsevier (Amsterdam).
33. Driesch H (1929) *The Science and Philosophy of the Organism*. A C Black (London).
34. Webster G, Goodwin BC (1982) The origin of species: A structuralist approach. *J Social Struct* 5:15–47.
35. Denton MJ, Marshall CJ, Legge M (2002) The protein folds as platonic forms: New support for the pre-Darwinian conception of evolution by natural law. *J Theor Biol* 219:325–342. doi:10.1006/jtbi.2002.3128
36. Fodor JA, Piattelli-Palmarini M (2011) *What Darwin Got Wrong*. Picador/Farrar, Straus and Giroux (New York).
37. Depew DJ, Weber BH (1996) *Darwinism Evolving: Systems Dynamics and the Genealogy of Natural Selection*. MIT Press (Cambridge, MA).
38. Wuensche A (2004) Basins of Attraction in Network Dynamics: A Conceptual Framework for Biomolecular Networks. In: Schlosser G, Wagner GP, eds. *Modularity in Development and Evolution*. University of Chicago Press (Chicago), pp 288–313.
39. Jonas H (2001) *The Phenomenon of Life: Toward a Philosophical Biology*. Northwestern University Press (Evanston, IL).
40. Paley W (2005) *Natural Theology, or, Evidences of the Existence and Attributes of the Deity*. Coachwhip Publications (Landisville, PA).
41. Descartes R (2003) *Treatise on Man*. Prometheus Books (New York).
42. Ray J (1717) *The Wisdom of God as Manifest in the Works of Creation*, 7th ed., corrected. R Harbin for William Innys (London).
43. Darwin C (1862) *The Various Contrivances by which Orchids are Fertilised by Insects*. John Murray (London).
44. Behe M (2006) *Darwin's Black Box: The Biochemical Challenge to Evolution*. 10th Anniv. ed., Free Press (New York).
45. Dembski W (2008) *The Design of Life: Discovering Signs of Intelligence in Biological Systems*. Foundation for Thought and Ethics (Dallas).
46. Meyer SC (2009) *Signature in the Cell: DNA and the Evidence for Intelligent Design*. HarperOne (New York).
47. Wagner GP (2006) How wide and how deep is the divide between population genetics and developmental evolution? *Biol Philos* 22:145–153. doi:10.1007/s10539-005-9011-9
48. Prum RO, Brush AH (2002) The evolutionary origin and diversification of feathers. *Q Rev Biol* 77:261–295. doi:10.1086/341993
49. Weismann A (1904) *The Evolution Theory*. Edward Arnold (Bristol, England).
50. Linde-Medina M (2011) Adaptation or exaptation? The case of the human hand. *J Biosci* 36:575–585. doi:10.1007/s12038-011-9102-5
51. Monod J (1972) *Chance and Necessity: An Essay on the Natural Philosophy of Modern Biology*. Translated by Austryn Wainhouse. Collins (London).
52. Crick F (2004) *Of Molecules and Men*. Prometheus Books (Amherst, NY).
53. Watson JD, Berry A (2003) *DNA: The Secret of Life*. Alfred A. Knopf (New York).
54. Keller EF (2000) *The Century of the Gene*. Harvard University Press (Cambridge, MA).
55. Henderson L (1913) *The Fitness of the Environment: An Inquiry into the Biological Significance of the Properties of Matter*. Macmillan Co. (New York).

56. Denton MJ (2013) The place of life and man in nature: Defending the anthropocentric thesis. *BIO-Complexity* 2013 (1):1–15. doi:10.5048/BIO-C.2013.1
57. Denton MJ (1998) *Nature's Destiny: How the Laws of Biology Reveal Purpose in the Universe*. Free Press (New York).
58. Davies PCW (1982) *The Accidental Universe*. Cambridge University Press (Cambridge, New York).
59. Barrow JD, Tipler FJ (1988) *The Anthropic Cosmological Principle*. Oxford University Press, (Oxford).
60. Gribbin JR, Rees MJ (1991) *Cosmic Coincidences*. Black Swan (UK).
61. Davies PCW (2004) *The Cosmic Blueprint: New Discoveries in Nature's Creative Ability to Order the Universe*. Templeton Foundation Press (Philadelphia).
62. Denton MJ, Marshall C (2001) Laws of form revisited. *Nature* 410:417. doi:10.1038/35068645
63. Rose GD, Fleming PJ, Banavar JR, Maritan A (2006) A backbone-based theory of protein folding. *P Natl Acad Sci USA* 103:16623–16633. doi:10.1073/pnas.0606843103
64. Chothia C, Hubbard T, Brenner S, Barns H, Murzin A (1997) Protein folds in the all- β and all- α classes. *Annu Rev Biophys Biomol Struct* 26:597–627. doi:10.1146/annurev.biophys.26.1.597
65. Weinreich DM, Delaney NE, DePristo MA, Hartl DL (2006) Darwinian evolution can follow only very few mutational paths to fitter proteins. *Science* 312:111–114. doi:10.1126/science.1123539
66. Singer SJ, Nicolson GL (1972) The fluid mosaic model of the structure of cell membranes. *Science* 175:720–731. doi:10.1126/science.175.4023.720
67. Waddington CH (1962) *New Patterns in Genetics and Development*. Columbia University Press (New York).
68. Ball P (2001) *The Self-made Tapestry: Pattern Formation in Nature*. Oxford University Press (Oxford, New York).
69. Ball P (2009) *Shapes: Nature's Patterns: A Tapestry in Three Parts*. Vol. 1. Oxford University Press (Oxford).
70. Edelmann JB, Denton MJ (2006) The uniqueness of biological self-organization: Challenging the Darwinian paradigm. *Biol Philos* 22:579–601. doi:10.1007/s10539-006-9055-5
71. Huttner WB, Schmidt AA (2002) Membrane curvature: A case of endofeelin'... *Trends Cell Biol* 12:155–158. doi:10.1016/S0962-8924(02)02252-3
72. Hyman AA, Karsenti E (1996) Morphogenetic properties of microtubules and mitotic spindle assembly. *Cell* 84:401–410.
73. Kirschner MW, Mitchison T (1986) Microtubule dynamics. *Nature* 324:621. doi:10.1038/324621a0
74. Nédélec FJ, Surrey T, Maggs AC, Leibler S (1997) Self-organization of microtubules and motors. *Nature* 389:305–308. doi:10.1038/38532
75. Karsenti E (2007) Self-organisation processes in living matter. *Interdiscipl Sci Rev* 32:163–175. doi:10.1179/030801807X163607
76. Tawk M, Araya C, Lyons DA, Reugels AM, Girdler GC et al. (2007) A mirror-symmetric cell division that orchestrates neuroepithelial morphogenesis. *Nature* 446:797–800. doi:10.1038/nature05722
77. Karsenti E (2008) Self-organization in cell biology: a brief history. *Nat Rev Mol Cell Biol* 9:255–262. doi:10.1038/nrm2357
78. Harold FM (1990) To shape a cell: An inquiry into the causes of morphogenesis of microorganisms. *Microbiol Rev* 54:381–431.
79. Mitchison TJ (1992) Self-organization of polymer-motor systems in the cytoskeleton. *Phil Trans R Soc B* 336:99–106.
80. Misteli T (2001) The concept of self-organization in cellular architecture. *J Cell Biol* 155:181–186. doi:10.1083/jcb.200108110
81. Harold FM (2005) Molecules into cells: Specifying spatial architecture. *Microbiol Mol Biol Rev* 69:544–564. doi:10.1128/MMBR.69.4.544-564.2005
82. Russell ES (1930) *The Interpretation Of Development And Heredity: A Study In Biological Method*. Oxford University Press (Oxford).
83. Lehn J-M (2002) Toward complex matter: Supramolecular chemistry and self-organization. *P Natl Acad Sci USA* 99:4763–4768. doi:10.1073/pnas.072065599
84. Whitesides GM, Grzybowski B (2002) Self-assembly at all scales. *Science* 295:2418–2421. doi:10.1126/science.1070821
85. Maderspacher F (2009) Form, force and flamboyance. *Curr Biol* 19:R743–745. doi:10.1016/j.cub.2009.08.032
86. Carroll S (2006) *Endless Forms Most Beautiful: The New Science of Evo Devo and the Making of the Animal Kingdom*. WW Norton & Co. (New York).
87. Zhu J, Zhang Y-T, Alber MS, Newman SA (2010) Bare bones pattern formation: A core regulatory network in varying geometries reproduces major features of vertebrate limb development and evolution. *PLoS ONE* 5:e10892. doi:10.1371/journal.pone.0010892
88. Sheth R, Marcon L, Bastida MF, Junco M, Quintana L et al. (2012) Hox genes regulate digit patterning by controlling the wavelength of a Turing-type mechanism. *Science* 338:1476–1480. doi:10.1126/science.1226804
89. Coen E (1999) *The Art of Genes: How Organisms Make Themselves*. Oxford University Press (New York).
90. Salthe SN (1993) *Development and Evolution: Complexity and Change in Biology*. MIT Press (Cambridge, MA).
91. Weber BH, Depew DJ (1996) Natural selection and self organization: Dynamic models as a clue to a new evolutionary synthesis. *Biol Philos* 11:35–65.
92. Nijhout HF (2002) The nature of robustness in development. *Bioessays* 24:553–563. doi:10.1002/bies.10093
93. Camazine S, Debubourg J-L, Franks NR, Theraulaz G, Bonabeau E (2003) *Self-organization in Biological Systems*. Princeton University Press (Princeton NJ, Oxford).
94. Gardner RL, Surani MA, Solter D (2003) Epigenesis versus preformation during mammalian development. *Introduction. Phil Trans R Soc B* 358:1313–1315. doi:10.1098/rstb.2003.1335
95. Keller R, Davidson LA, Shook DR (2003) How we are shaped. *Differentiation* 71:171–205. doi:10.1046/j.1432-0436.2003.710301.x
96. Hinchcliffe JR (2002) Developmental basis of limb evolution. *Int J Dev Biol* 46:835–845.
97. Gilbert SF, Singer S (2006) *Developmental Biology*, 8th ed. Sinauer (Sunderland, MA).
98. Davis GK, Patel NH (2002) Short, long, and beyond: Molecular and embryological approaches to insect segmentation. *Annu Rev Entomol* 47:669–699. doi:10.1146/annurev.ento.47.091201.145251
99. Liu PZ, Kaufman TC (2005) Short and long germ segmentation: Unanswered questions in the evolution of a developmental mode. *Evol Dev* 7:629–646. doi:10.1111/j.1525-142X.2005.05066.x
100. Alvarado AS, Tsonis PA (2006) Bridging the regeneration gap: Genetic insights from diverse animal models. *Nat Rev Genet* 7:873–884. doi:10.1038/nrg1923
101. Gilbert SF (2010) *Developmental Biology*, 9th ed. Sinauer Associates (Sunderland, MA).
102. Denton MJ (1986) *Evolution: A Theory in Crisis*. Adler and Adler (Bethesda, MD).
103. deBeer GR (1971) *Homology, An Unsolved Problem*. Oxford University Press (Glasgow).
104. Newman SA, Bhat R (2009) Dynamical patterning modules: a “pattern language” for development and evolution of multicellular form. *Int J Dev Biol* 53:693–705. doi:10.1387/ijdb.072481sn
105. Fleury V (2009) Clarifying tetrapod embryogenesis, a physicist's point of view. *Eur Phys J Appl Phys* 45:30101. doi:10.1051/epjap/2009033
106. Cherniak C (1994) Component placement optimization in the brain. *J Neurosci* 14:2418–2427.
107. Cherniak C, Mokhtarzada Z, Rodriguez-Esteban R, Changizi K (2004) Global optimization of cerebral cortex layout. *P Natl Acad Sci USA* 101:1081–1086. doi:10.1073/pnas.0305212101

108. Cherniak C (2009) Brain wiring optimization and non-genomic nativism. In: Piattelli-Palmarini M, Uriagereka J, Salaburu P, eds. *Minds and Language: A Dialogue with Noam Chomsky in the Basque Country*. Oxford UP (Oxford), pp 108–119.