

The uniqueness of biological self-organization: challenging the Darwinian paradigm

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Abstract Here we discuss the challenge posed by self-organization to the Darwinian conception of evolution. As we point out, natural selection can only be the major *creative* agency in evolution if all or most of the adaptive complexity manifest in living organisms is built up over many generations by the cumulative selection of naturally occurring small, random mutations or variants, i.e., additive, incremental steps over an extended period of time. Biological self-organization—witnessed classically in the folding of a protein, or in the formation of the cell membrane—is a fundamentally different means of generating complexity. We agree that self-organizing systems may be fine-tuned by selection and that self-organization may be therefore considered a complementary mechanism to natural selection as a causal agency in the evolution of life. But we argue that if self-organization proves to be a common mechanism for the generation of adaptive order from the molecular to the organismic level, then this will greatly undermine the Darwinian claim that natural selection is the major *creative* agency in evolution. We also point out that although complex self-organizing systems are easy to create in the electronic realm of cellular automata, to date translating *in silico* simulations into real material structures that self-organize into complex forms from local interactions between their constituents has not proved easy. This suggests that self-organizing systems analogous to those utilized by biological systems are at least rare and may indeed represent, as pre-Darwinists believed, a unique ascending hierarchy of natural forms. Such a unique adaptive hierarchy would pose another major challenge to the current Darwinian view of evolution, as it would mean the basic forms of life are *necessary* features of the order of nature and that the major pathways of evolution are

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determined by physical law, or more specifically by the self-organizing properties of biomatter, rather than natural selection.

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Few doubt that the self-organization of matter generates much of the complexity of the inorganic world, from molecules to galaxies (Haken 1977; Yates et al. 1987; Bak 1996; Ball 1999; Lehn 2002). That self-organization is also exploited by living systems is evident in the formation of proteins (Anfinsen 1973), the formation of the spindle apparatus and other microtubular forms (Kirschner and Mitchinson 1986; Nedelec et al. 1997; Surrey et al. 2001), the cell membrane and various vesicular forms (Singer and Nicholson 1972; Trinkaus 1984), and in the construction of the nests of social insects (Franks et al. 1992; Camazine et al. 2001). The possibility that self-organization might be a general mechanism for generating robust adaptive complexity—at all levels of the biological hierarchy, from the molecular to the organismic—is evidenced by the current interest in the subject in many different fields, including cell biology (Mitchinson 1992; Harold 2001; Misteli 2001), developmental biology (Nijhout 1990; Salthe 1993; Goodwin 1994: ch. 4 and 5; von Dassow et al. 2000; Newman 2002; Gardner et al. 2003; Keller et al. 2003), the origin of life (Kauffman 1993; Weber 1998; Woolfson 2000: ch. 11) and the evolutionary origin of organic form (Lewin 1992: 32–43; Newman 1993; Salazar-Ciudad et al. 2001a, b; Newman 2002). Given the adaptive advantages of self-organization as a means of generating complexity, including its genetic economy (Camazine et al. 2001: 38–39, 63) and robustness (Camazine et al. 2001: 37, 337–338) we believe it likely that self-organization will turn out to be used by living organisms in many different types of biological systems.

Despite the increased awareness and acknowledgement of the biological significance of self-organization by authors in so many different fields, many evolutionary biologists appear to down play its implications and role in evolution. Indeed several recent publications by convinced Darwinists, including Richard Dawkins (1976, 1986, 1996, 2004), Mark Ridley (1997) Kenneth Miller (1999) and Ernst Mayr (2001) contains no reference to the mechanism at all. Even Gould (2002: 1208–1214) devotes only a few pages to the phenomenon in his comprehensive study of evolution—*The Structure of Evolutionary Theory*—while discussing the views of Brian Goodwin and Stuart Kauffman. However, a number of evolutionary biologists have begun to explore a reconciliation between self-organization and neo-Darwinism. These authors generally concede that self-organization and natural selection are two different mechanisms for generating biological complexity—self-organization providing adaptive order “for free,” natural selection generating “hard earned” adaptive order which is decidedly “not for free”—yet see the two mechanisms as essentially complementary (Weber and Depew 1996; Kauffman 1993: 409; Camazine et al. 2001: ch. 3; Ruse 2003: ch. 9; Maynard Smith and Szathmary 1999: 115–116; Conway Morris 2003: 204–205).

Although we agree that self-organization and cumulative selection may operate cooperatively in adaptive evolution, we argue that where complex adaptive order is generated by self-organization (we discuss below many cases of this that are now well characterized), this does pose a challenge to the standard Darwinian paradigm,

and particularly to the core claim of classic Darwinism (as defined by Darwin 1872; Dawkins 1986; Dennett 1995; Gould 2002: ch. 2; Ruse 2003) that gradual cumulative selection is the major or sole *creative agent* responsible for the evolution of organic form and biological complexity—that most biological complexity is hard earned. We argue that natural selection can be responsible for the *preservation* of self-organized adaptive complexity once it has arisen, that it may assist its spread though a population and it may fine tune it in various adaptive directions or canalize developmental processes by the replacement or enhancement of initially self-organized systems by hard wired genetic circuits as Stuart Newman has argued (Newman 1993, 1994), but it *cannot be the creator* of that complexity in the first place. Consequently, despite the complementary nature of the relationship, the greater the role of self-organization in the generation of life's adaptive order, the less the *creative* role of cumulative selection and the less the overall evolutionary process can be strictly termed “Darwinian.”

We also consider the possibility that the self-organizing systems may represent a unique hierarchy of adaptive forms, ascending from the molecular to the organismic level, without any analog outside the realm of life. Such a view echoes a common pre-Darwinian conception that organic forms represent a finite set of “lawful natural forms,” like crystalline forms, built into nature and part of the world order no less than the forms of the inorganic world from, atoms to galaxies (Schwann 1847; Chambers 1844; Aggasiz 1874; Owen 1866; Gould 2002: ch. 4). Few recent authors have considered this possibility. We believe this is mainly because of an anti-vitalistic tendency among biologists, witnessed in the almost universal assumption—even among those who have recently stressed the role of self-organization in evolution (Langton 1989; Levy 1993: 93–120; Lewin 1992; Kauffman 2000)—that life is not special or unique to the organic world; that many alternative life forms are possible or may be—indeed will be—synthesized in the lab in the near future (Langton 1989; Levy 1993; Kauffman 2000).

However, as we argue below, after a century of spectacular scientific advances, no natural self-organizing systems remotely analogous to those of biology have been discovered and no artificial *material* systems have been created that exhibit self-organizing properties as elegant and complex as those exploited by living systems. This suggests that complex adaptive self-organizing systems are likely to be rare in the total space of all possible complex material systems, and it lends support to the possibility that the self-organizing systems of biology are unique. This is a possibility that would pose an additional and particularly severe challenge to the *creativity* of natural selection. For, if there is only one natural hierarchy of self-organization for life to exploit, selection would have no choice and evolution's paths and patterns would not be as Darwinists have always implied: historic and contingent (Monod 1972: 49; Kauffman 1993: 5; Gould 2002: 1332–1343), but necessary and preordained as was believed before Darwin. Because natural selection would have no choice, rewinding the tape of evolution—Gould's (1989: 48) “great undoable experiment”—however, many times would not result in radical novelty, as Gould and other Darwinists like John Maynard Smith (1992: 35) have argued. Thus, “pure chance, blind and free” would not “lie at the very root of evolution” as Jacques Monod famously claimed (1972: 110).

Cumulative selection

In his *The Structure of Evolutionary Theory*, Gould (2002: 140) points out in an incisive analysis of the core logic of Darwinism that natural selection can only play a *creative* role in *molding* evolutionary forms if two stringent conditions are met:

“(1) if nothing about the provision of the raw materials—that is, the sources of variation—imparts direction to evolutionary change; and (2) if change occurs by a long and insensible series of intermediary steps, each superintended by natural selection—so that “creativity” or “direction” can arise by the summation of the increments.”

If these two conditions hold, and all Darwinian advocates assume that they do, then natural selection can be conceived of as Darwin did in the *Origin*: as the sole director and creative agent in evolution, responsible for all the complexity of life and the phylogenetic branching pattern of the tree of life, which can be presumed to be entirely undirected and contingent. Hence, the claim above that rewinding the tape would produce a completely novel tree of life.

Expanding on the view that “nothing about the provision of variation imparts direction to evolution” (condition 1) Gould (2002: 141) continues:

“Variation must exist in sufficient amount, for natural selection *can make nothing*, and must rely upon the bounty thus provided (by natural variation) but variation must not be too florid or showy either, lest it become the creative agency itself. Variation in short must be *copious, small in extent, and undirected*” [our emphasis].

Expanding on the necessity that the individual variations—the raw material on which selection acts—be small Gould (2002: 143) comments further:

“If the variations that yielded evolutionary change were large—producing new major features, or even new taxa in a single step then natural selection, as a theory of evolutionary causation, would perish because variation itself would emerge as the truly creative force. This is why saltational and macromutational theories have always been viewed within the evolutionary community as anti-Darwinian.”

Commenting on the necessity that evolutionary change occurs via a long series of incremental steps (condition 2) Gould (2002: 150) expands:

“We now come to the heart of what natural selection requires ... in going from A to a substantially different B, evolution must pass through a long insensible sequence of intermediate steps—in other words, that ancestor and descendent must be linked by a series of changes, each within the range of what natural selection might construct from ordinary variability. Without gradualism in this form, large variations of discontinuous morphological import—rather than natural selection—might provide the creative force of evolutionary change.”

Over and over again in the *Origin* Darwin stressed that evolution by natural selection is an extremely gradual process (1872: 146, 156, 413–414). His several references to the aphorism *Natura non-facit saltum* (1872: 156, 414) highlight his commitment to an intensely gradualistic scheme. He was insistent not only that the process is very gradual, but that the individual variants upon which selection acts are

very small. Indeed in the *Origin* (1872: 32) he talks of the differences that natural selection exploits as being “absolutely inappreciable by an uneducated eye—differences which I for one have vainly attempted to appreciate.” Holding the individual steps to be so extremely small, it is no wonder Darwin (1872: 407) envisaged the building of organic complexity to have required “an *interminable series* of intermediates” [our emphasis].

Darwin’s central and entirely unique claim in the *Origin* was not that natural selection occurs and is bound to eliminate the unfit—all his colleagues and predecessors accepted this postulate (Gould 2002: 139; Gale 1972). Nor was there anything revolutionary about Darwin’s claim that descent with modification occurs—many of his predecessors including Lamarck, Robert Chambers and Richard Owen all accepted some version of this. Rather, his revolutionary claim was that natural selection could be the main *creative agent* in evolution if it superintended the ever so gradual accumulation of tiny undirected mutations (Wicken 1986: 23). Selection per se is not the defining characteristic of Darwinism, but only where it acts as the creative agent, building complexity incrementally resulting in what Gould (2002: 629) terms “additive aggregates.”

Stated more formally, natural selection can be the *creative agent* in evolution, as Darwinists claim, only if all or nearly all of the adaptive complexity of biological systems (**C**) is the result of the cumulative selection, over many “interminable” generations, of small, undirected, advantageous, “ordinary” microvariants [“ordinary” meaning those variations that are observed to occur naturally within populations of organisms]. Thus **a + b + c + d = C** (Darwin 1872; Williams 1966; Dawkins 1986; Dennett 1995). Darwinian complexity built up by natural selection is hard earned and additive, each step accomplished as Dennett describes (1995: 75): “by brute, mechanical ... climbing from the base already built by the efforts of earlier climbing.” Thus, complexity achieved in a single sudden step, what Dawkins called “single step selection” (Dawkins 1986: ch. 3), or where the individual steps are larger than the usual variants that occur in any population (Gould 2002: 143), indeed all complexity not earned the hard way by gradual cumulative selection must be termed “non-Darwinian.” Indeed as Dawkins (1986: 318) argues in the final paragraph of the *Blind Watchmaker* to deny slow gradualism is to “deny the very heart of [Darwin’s] evolution theory.”

Self-organization

In their book *Biological Self-organization* Camazine et al. (2001: 8) define self-organization:

“As a process in which pattern at the global level of a system emerges solely from numerous interactions among the lower level components of the system. Moreover the rules specifying interactions among the system’s components are executed using only local information, without reference to the global pattern. In short pattern is an emergent property of the system rather than being imposed on the system by an external ordering influence.”

The examples of self-organized complexity dealt with in Camazine et al. (2001), such as insect nests, honey combs, foraging army ant columns are all examples of dynamic far from equilibrium energy dissipating self-organizing systems. This is the type of

self-organization that most authors in the field refer to when they discuss the phenomenon (Wiley and Brooks 1982; Wicken 1987; Weber and Depew 1996; Camazine et al. 2001; Barth et al. 2005). However, not all self-organizing systems in biology are far from equilibrium energy dissipating systems, like an ant nest. As Whitesides and Grzybowski (2002) point out, forms such as the protein and RNA folds and membrane forms are no less self-organizing than an ant's nest, but they are systems at a global or local equilibrium (energy minimum) which involve dynamic interactions between their components during their formation and require energy to reach their final adaptive conformation. However, once formed they do not require a continual input of energy for their maintenance. Because these forms crystallize spontaneously, as a result of local interactions between their components, and because they are uninfluenced by an external ordering principle, they must be deemed self-organizing.

We believe that the Camazine definition—which covers both energy dissipating and non-energy dissipating self-organized systems (Whitesides and Grzybowski 2002)—is a good working definition of biological self-organization and the one we have adopted here. We believe it captures the essence of the phenomenon, which is the spontaneous generation of complexity by a system of interacting components without external ordering influences.

The term “solely” in the Camazine definition quoted above presumes a closed system. But of course no self-organizing system in biology or physics is perfectly closed, at least thermodynamically. All organisms are complex, far from equilibrium systems or dissipative structures (Wiley and Brooks 1982; Depew and Weber 1988). Nonetheless many biological self-organizing systems organize themselves with only minimal input from outside, apart from energy. Organisms and their component self-organizing systems are as Wiley and Brooks (1982) comment, “open ended in terms of energy and closed in terms of information and cohesion.” That they are indeed closed in terms of *information* and cohesion and uninfluenced by any external informational input is indicated by the increasing success in artificially simulating protein folding (Srinivasan and Rose 2002; Chivian et al. 2003), the formation of insect nests (Camazine et al. 2001), and microtubular cytoarchitectural forms (Nedelec et al. 1997; Surrey et al. 2001) in computers. These programs solely involve rules that define the interactions between lower level components and the self-organized complexity in these cases is arising solely from the rules that define lower level interactions—there is no external input of information! Moreover, in the case of protein folding (Anfinsen 1973), aster formation (Nedelec et al. 1997) or insect nest formation (Camazine et al. 2001) these can be observed *in vitro* in isolated systems consisting only of the constituents of the self-organizing system itself where all environmental physical or chemical influences have been excluded.

The Camazine definition of self-organization excludes the various types of ontogenetic selection discussed by Deacon (1997), which are very widely considered to play a role in neural development (Karmiloff-Smith 1992; Deacon 1997; Shatz 1996; Johnson 1997; Karmiloff-Smith 2001). The process as envisaged by Deacon (1997) is in essence Darwinian—a version of cumulative selection. In fact Deacon (1997: 202) himself calls it “selective elimination,” involving the functional improvement of the system in incremental steps. Crucially, the order generated by incremental functional optimization is not spontaneous and for free, it is hard earned and acquired gradually after a series of trials. Moreover the overall process is one in

which selection acts as an external force guiding the neuronal connections into a functionally optimized network.

The Camazine definition also excludes self-assembly as witnessed in systems such as viral capsid assembly, the assembly of the ribosome and other cellular machines (Kalthoff 1996). In all such cases the assemblage is essentially a 3D jigsaw and the final form is the predicted end or the sum of its parts. Camazine et al. (2001: 29) concur that global pattern arising from the assembly of a set of prefigured parts of a particular shape is not self-organization because it does not require the “continual interactions among lower level components to maintain structure.” Edelman (1987: 124) has also drawn a contrast between self-organized pattern that involves dynamic interactions between components, and the prefigured and static pattern of a jigsaw that is imposed on the jigsaw from outside. In the assembly of a jigsaw no new “order for free” is generated by the interactions between the pieces—the only order that emerges was already explicit in the shapes of the pieces themselves.

The term self-organization is often used loosely in the literature of supramolecular chemistry or nano technology and applied to cases of self-assembly or self-ordering where the final order of the structure, as in the recent fascinating example of DNA “origami” (Rothemund 2006) is pre-specified in detail in the starting fragments. These processes are examples of self-assembly, or as described by Rothemund, cases of “bottom up fabrication” and *not self-organization*. Similarly, Barth et al. (2005) in their *Nature* review of nano surface structures are careful to point out that the remarkable achievements in engineering nano structures are examples of “self-ordering” matter and not self-organization.

In all self-organizing systems the final emergent complex global form **C** (often referred to in the terminology of dynamic systems as the *attractor* of the system), arises from the spontaneous interactions of its components, **a**, **b**, **c**, and **d** (Camazine et al. 2001: 32). In the case of self-organization the form and properties of **C** are not built up bit-by-bit gradually by the simple linear addition of successive incremental steps—i.e., of **a + b + c + d**—but arise out of complex non-linear interactions (Strogatz 1994: 9) involving various types of self-reference and feedback (Gleick 1998: 167–68; Gribben 2005: 79). Being genuinely emergent, **C** is more than the linear sum of its parts. Rather, we may more properly represent **C** as **a*b*c*d**. The process is more akin to a sudden phase transition (Kauffman 2000: 35; Florey 1969; Haken 1977) rather than any sort of incremental stepwise process. The unexpected emergence of self-organized complexity has been described as “magic” by Kauffman (2000: 35, see also Lewin 1992: ch. 2) and something of its “magical” quality is illustrated by the complex emergent patterns—sometimes fantastically intricate—generated by cellular automata programmed to follow remarkably simple rules (Levy 1993; Wolfram 2002).

Cumulative selection (Darwin 1872; Dawkins 1986; Dennett 1995) is therefore a completely different and far more prosaic mechanism—as far from something like a phase transition as can be imagined. The realm that selection rules is a predictable realm characterized by intermediates, continuity and gradual linear additive functional transitions. On the other hand, the realm of self-organized complexity is an unpredictable realm of sudden spontaneous emergent complexity that is generated by non-linear interactions via something like a phase transition. This is a realm where saltation, emergence, spontaneous sudden change and bifurcations rule; a realm in which the concepts of intermediacy, gradualism and continuity, so central to the Darwinism, no longer apply. In Misteli’s words (2001: 183):

“Typically self-organized systems undergo transitions which occur suddenly and typically without intermediates. Self-organized systems are frequently in a state of criticality; that is, a point at which systems properties can undergo sudden change. Transitions between distinct assembly patterns are not gradual but sharp.”

You can assemble a LEGO toy bit-by-bit through cumulative selection, but you cannot gradually cross bit-by-bit the “phase transition” that separates the pre-organized constituents of a self-organized system from their post self-organized newly emergent form. The “good design” (Dennett 1995: 144) generated by selection is “hard earned” over time; self-organization is unearned “for free” (Kauffman 1993).

Generating adaptive complexity by cumulative selection is climbing “mount improbable” gradually in hard earned steps over perhaps thousands of generations (Dawkins 1996). Generating adaptive complexity by self-organization is climbing mount improbable in one saltational step! Cumulative selection may gradually put together or fine tune the physical properties of each of the individual constituents **a**, **b**, **c**, and **d** of a self-organizing ensemble, but not the collective property of the ensemble (**a*b*c*d**) to self-organize into the emergent higher order structure **C**. This collective property depends on the temporal and spatial co-presence of all the constituents of the ensemble in a particular physiological environment. For this reason classic cumulative selection can never be the determining *cause* of the emergent complexity (or indeed of any emergent properties) generated by self-organization in any complex system.

Although all authors agree that the two mechanisms are quite different, there are many different perceptions of the relationship between natural selection and self-organization, and their relative contribution to adaptive evolution. Weber and Depew (1996: 44–45) distinguish seven perceptions, including “natural selection not self-organization drives evolution,” “self-organization is an auxiliary to natural selection in causing evolutionary change,” and their own perception that “natural selection and self-organization are two aspects of a single evolutionary process” and thus are “causally intertwined.” Our perception of the relationship is very similar to Camazine et al. (2001); that it is fundamentally cooperative, in which “natural selection molds the complex ends achieved by self-organization,” by molding “the rules of interaction of the components (Camazine et al. 2001: 89).” We see the relationship as inevitably cooperative, as no biological self-organizing system can escape the continual scrutiny of selection. We think that this is the common sense view. However, we believe that given the diversity of self-organizing systems (some are energy dissipating) while others are non-energy dissipating (proteins and membrane forms), and because the stringency of the criteria for self-organization may vary, *generalizing* the relationship between selection and self-organization is difficult. In some cases self-organization may depend on very exact conditions—i.e., self-organization will only occur where there exists the co-presence of a very special (nearly unique) set of constituents, in which case there is very little scope for natural selection to tune the parameters of the system. In other cases (such as insect nests) the criteria may be less stringent and there may be ample room for selection to creatively fine tune the parameters and mold the final emergent form. The degree to which natural selection can fine-tune self-organized adaptive order and the fundamental nature of the relationship will therefore vary depending on the actual material system under consideration. In the case of an ant’s nest, rule changes may

play a very influential role in changing the emergent order in various adaptive directions. A great deal of further empirical work is needed to validate any particular position regarding the relationship in specific cases.

We note in passing that the existence of self-organization and the resultant emergent order it generates in living systems not only challenges the all sufficiency of cumulative selection as the sole or major evolutionary mechanism, it also challenges the other great assumption of 20th century biology: the conception that the complex 3D form of organisms is specified in detail in a DNA program. There is of course a deep and necessary connection between Darwinism and the idea of detailed specification in the genes. It was August Weismann (1902) who first saw so clearly that because cumulative selection builds an organic order that is artifactual, additive and contingent—LEGO like—then its re-specification in each generation necessitates (as does the re-specification of any contingent, additive material assemblage like a machine or LEGO toy) a blueprint of program specifying its design in detail bit-by-bit during development. The generation of unearned (by selection) order sits uneasily with the gene-centric-pre-formational conception of neo-Darwinism, which holds everything is programmed or prefigured in the genes. Self-organized order is indeed genuinely epigenetic and not necessarily in the genes at all, although the basic individual components comprising the ensemble that self-organizes into the global emergent form are specified in the genome. However, the emergent form and the interactions between the participants are only implied. The emergent forms generated by self-organizing systems—protein folds, microtubular forms, etc.—were not created gradually, additively or contingently by natural selection, nor are they specified bit-by-bit in detail in the genome. Neo-Darwinian complexity necessitates self-specification by the genes, not self-organization by the products of the genes!

Of course in the absence of any evidence that cellular or organismic complexity is largely the result of detailed genetic specification (Keller 2000), mainstream biology and many Darwinists reject Weismann's strict blueprint model. Dawkins (1986) and Ridley (2004) for example see the specification as coming about more from a "genetic recipe," a sequence of instructions on how to build an organism, rather than from a blueprint, consisting of a compact spatial temporal representation of its design. The orb web of a spider and many structures built by insects, such as the funnel guarding the entrance of the mud wasp's nest, are all built by following a recipe (Camazine et al. 2001: ch. 4). Accepting a recipe is a tacit admission of the importance of epigenetic processes in development. It is also a tacit admission that organisms are more than mere additive aggregates, as Weismann conceived of them. Rather, it admits that that an organism's complexity cannot be condensed or described in a bit-by-bit specification.

Self-organization sits uneasily therefore, not only with classic Darwinian cumulative selection, but also classic 20th century "gene centrism" (Keller 2000) because the complexity it generates is decidedly non-additive and cannot be by its fundamental nature the result of any sort of detailed genetic specification. Given the spontaneous and emergent nature of self-organization it is little wonder that the concept has not been received enthusiastically by mainstream Darwinists. As Gould (2002: 1213) comments, we have "been so tuned to other, largely reductionist, modes of thought, that the conceptual tools [to handle the idea of emergent self-organized complexity] have never been developed."

Emergence

The global order or whole (e.g., the 3D form of a protein) generated by the self-organization of an ensemble of lower level constituents ($\mathbf{a*b*c*d}$) and the qualitatively new properties that are generally associated with the new whole are termed “emergent.” This is because they are difficult to predict from below, and cannot be understood in terms of a simple linear addition of the individual contributions of the constituents, i.e., they are not additively complex as in Darwinian systems. The fact that the emergent order of self-organization is unexpected and unpredictable—yet adaptive—serves only to emphasize the challenge to the orthodox Darwinian claim that cumulative selection is the sole agency responsible for adaptive order.

However, the fact that emergent properties are unexpected does not imply that there is any deep mystery to the phenomenon. As Camazine et al. (2001: 91) comment: “because the [emergent] properties of the system often defy intuitive understanding, those properties may seem to appear mysteriously... [but] there is nothing mystical or unscientific about emergence.” Folded proteins, ants nests, microtubular cyto-structures like the spindle, etc., arise from complex (and difficult to compute) dynamic interactions between their parts (amino acids, ants, etc.). These wholes are self-evidently more than the additive sum of their parts but *no* more than the dynamic sum of the interactions of their components, intractable those these may be. They are well described within the terms and framework of mainstream dynamic systems theory.

Although the form and property of such emergent wholes cannot be predicted accurately, progress is being made towards that end. In the realm of protein prediction, for example, understanding the rules which determine protein form may ultimately allow the *ab initio* prediction of 3D form from sequence. Already hierarchic prediction programs like LINUS (Srinivasan and Rose 2002) and ROSETTA (Chivian et al. 2003), based primarily on consideration of rules that determine local interactions (for example, steric constraints which restrict the conformation of short sections of the polypeptide chain), are able to predict higher order structures with remarkable accuracy. Computer simulations of the self-organization of microtubular forms (Surrey et al. 2001) and insects’ nests (Camazine et al. 2001) based on an understanding of the “local interaction rules” are also yielding successes. In all these instances emergence is a practical rather than an in-principal challenge.

To summarize, the challenge to Darwinism posed by self-organization is that it generates emergent patterns—whatever their precise ontological status—which represent adaptive complexity that spontaneously arises from the dynamic interactions between a set of material components. Self-organized order is spontaneous pattern from within; the order of selection is additive order from without.

Self-organization: from proteins to insects’ nests

The first set of important biological structures shown as the result of self-organization were the protein folds. Their ability to self-organize into their complex 3D native forms, without assistance from any outside agency, was indicated by Anfinsen’s (1973) work in the 1950s on the renaturation of the enzyme ribonuclease.

Anfinsen's and subsequent work has shown that the formation of the native form of a protein is created by energy minimization resulting from local interactions between the amino acids in the linear polypeptide chain (Srinivasan and Rose 2002; Chivian et al. 2003). The complex 3D forms of proteins are not specified in a genetic program but arise epigenetically via self-organization (Monod 1972: 89–97). The process of folding is basically a phase transition (Florey 1969) between the initial disordered chain and the tightly packed 3D crystal like form of the native conformation. Each of the approximately 1,000 folds represents a primary natural self-organizing form (like an atom or crystal) and adaptations are clearly secondary modifications of a primary form given by physics (Denton and Marshall 2001; Denton et al. 2002).

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 (Singer and Nicholson 1972). The same basic membrane structure makes up the endoplasmic reticulum, encloses the nucleus, the mitochondrion, the chloroplast and so forth. Lipid membranes form a vast variety of tubes, vesicles and various types of sheets. This diversity was described by Waddington (1962: 105–107):

“Membrane surfaces may assume a large variety of different forms...The tube may be considered a vesicle in which one dimension is very much elongate. Vesicles may be two skinned, and sometimes compressed into layered structures [the grana of chloroplasts]...the majority of subcellular organelles are built up as complexes of vesicles, diderms (two skinned vesicles), and tubes. Golgi bodies consist of piles of flattened vesicles mitochondria are complex closed vesicles constructed out of two membranes.”

All this plethora of forms arises spontaneously by self-organization from the physical properties of various bilayer lipid membranes of differing chemical composition. Different lipids and proteins can bend and distort the basic membrane form into various globular forms, vesicular forms or tubules (Huttner and Schmidt 2002). The various forms arise again like the protein folds entirely from the local interactions between membrane constituents. A zoo of vesicular forms can be generated spontaneously from lipid membranes depending on the ratio of lipid and protein constituents. This is the focus of a lot of current work. As Huttner and Schmidt (2002: 155) comment: “The shape of biological membranes reflects the shape of its principle constituents—that is membrane lipids and integral membrane proteins, as well as their interaction with each other and with peripherally associated proteins (including the glycoproteins and proteoglyans), the cytoskeleton and the extracellular matrix.” And reporting some fascinating work on a membrane altering protein dynamin they (2002: 156) 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 the DNA. All spontaneously emerge by self-organization from particular categories of matter in a process analogous to a phase transition.

The protein folds (and RNA folds) and the various lipid vesicular forms are classic examples of static self-organizing systems at global or local equilibrium which may require energy to form, but once formed do not require an input of energy to

maintain their forms. The other class of self-organizing systems exploited by organisms are dynamic and energy dissipating, where the maintenance of the final complex form is dependent on a continual consumption of energy (Whitesides and Grzybowski 2002). The classic type of a dynamic energy dissipating self-organizing system is the spindle apparatus.

That self-organization plays an important role in the assembly of various cytoskeletal structures, such as the microtubular aster and the spindle apparatus, has become clear as a result of landmark studies by a variety of researchers over the past two decades (Kirschner and Mitchison 1986; Michinson 1992; Nedelec et al. 1997). At each cell division the spindle apparatus organizes itself out of a seeming chaos of microtubules and molecular motors. Kirschner and Mitchison (1986) write:

“Dynamic instability produces a rapid turnover of microtubule configurations and intermediate structures produced during prometaphase in genetically identical cells are highly variable. This variability goes far beyond thermal fluctuations, so that in each cell division a different sequence of structures is produced in the pathway of spindle morphogenesis. The most stable configuration at metaphase is reached *not by following a map* [or detailed genetic blueprint] *but by following a gradient of increasingly more stable structures*” [our emphasis].

In other words, the final self-organized form represents some sort of natural free energy minimum or *attractor* that draws the components of the aster into what is a preferred or lawful conformation. The aster is not the only microtubular form, which arises by the self-organization of microtubules and molecular motors. Merely by altering the relative concentration of the motor protein kinesin and tubulin it is possible to generate a variety of microtubular forms in vitro (Nedelec et al. 1997). There is now a growing consensus that a great deal of the cytoarchitecture of the cell is generated by the self-organization of the cytoskeleton (Misteli 2001).

And self-organization extends far beyond the level of the cell. Self-organization is even exploited at the supra organismic level. The intriguing work of Deneubourge, Theraulaz, Bonabeaux, Camazine and colleagues (Camazine et al. 2001) and of others including Franks et al. (1992) on various structures built by social insects, including termite’s nests (Camazine et al. 2001: ch. 18) and the combs of honey bees (Camazine et al. 2001: ch. 16) has revealed that in many cases these structures are not the result of any externally imposed plan. Rather they arise from simple behavioral rules that determine the interactions between lower level components. In short they are classic cases of self-organized complexity. The enormous complexity of structure that can be generated from local interactions between the insects is witnessed graphically in the “truly awe inspiring” (Camazine 2001: 377) six meter high nests of tropical termites, and the immense nests of the tropical leaf cutter ants which may have a volume of 20 m³ and house up to 10 million individual ants (Holldobler and Wilson 1990).

These various developments have established that self-organization is indeed exploited by living organisms to generate complex form, from the molecular and cellular levels to the supra organismic level (in the case of the nests of social insects). In the context of these developments there can no longer be any doubt that detailed genetic specification is not the only mechanism for the generation of high degrees of complexity in biological systems.

Adaptive advantages of self-organization: robustness and genetic economy

One compelling reason for believing that self-organization may be very widely exploited by organisms is the *self-formative robustness* characteristic of all self-organized complexity (Camazine et al. 2001: 338). This is an enormous, and we believe, decisive adaptive advantage over non-self-organized complexity such as that exhibited by our own artifacts (such as watches or other sorts of machines), which must be mechanically put together bit-by-bit under the direction of a blueprint or program and if damaged they must be repaired by an outside agency, external to the system itself.

Consider the advantages that accrue to the cell from the self-formative robustness of proteins. Firstly, the cell is relieved of the enormous burden of having to specify and organize the fabrication and assembly of 1,000 complex 3D atomic architectures—a process that would be costly in energetic and informational terms. In effect the cell gets 1,000 immensely complex atomic forms that unerringly assemble into their proper native conformations billions of times each second. Secondly, as self-organizing forms, each fold is able to maintain and regain its native conformation in the turbulent chaos of the cell's interior, which may involve anything from the movement of a few atoms to the unfolding of sections of the amino acid chain (Brandon and Tooze 1999). Thus the cell has no need of any complex repair algorithms involving sensors, feed back control and special “repair machines” to reassemble them into the “proper configuration” after deformation. To get its tool kit of protein forms the cell needs only to specify linear amino acid sequences and the environmental conditions for their folding—the right pH, ionic strength etc. Moreover, because the folding is a process of energy minimization, the cell needs to expend no energy on the actual folding process. Once the linear sequences of amino acid and nucleotide residues have been chemically linked, nature provides both the three-dimensional complexity of the forms *and* the thermodynamic energy for their assembly. Unlike virtual automata, “nano assemblers,” (Drexler 1986) or macro-scale machines such as Lipson and Pollack's (2000) robotic life forms, the programs specifying the protein folds (the linear nucleotide sequences of the genes) are vastly *less complex* than their 3D structures.

The natural robustness of proteins has another consequence. The authors of a recent paper comment (Przytycka et al. 1999): “A protein's function is due to a comparatively small number of residues, suitably interspersed throughout the sequence. This process of embedding functional residues in a robust framework constitutes a versatile mechanism to confer multiple functions upon a given fold.” The folds are thus able to maintain their core architectures in the face of considerable amino acid sequence variation, and this contributes another important element of fitness. It makes possible adaptive substitutions that do not disrupt the underlying fold architecture and this facilitates functional molecular evolution. It is the generic robustness of the basic fold frameworks that permit such sequential “tampering” and consequent functional variation.

Consider next the adaptive advantages that accrue to the cell from the self-organizing property of the cell membrane. It is very difficult to imagine how the cell could be bounded by a non-self-organizing membrane structure, in fact any type of structure other than the lipid bilayer (Trinkaus 1984: 51–53). It is worth considering for a moment the problems that would be involved in attempting to coat the cell with

a non-self-organizing mechanical barrier made up of plates assembled bit-by-bit using an enzyme to splice adjacent plates together like the tiles that cover the space shuttle. [The fact that the tiles proved faulty in two of the most recent shuttle launches is an interesting reminder of the lack of robustness of mechanical constructs compared with the evident robustness of self-organizing natural forms like the cell membrane or the protein folds.] To begin with, it would require a complement of special enzymes to glue the tiles together. It would require that the tiles be transported to the cell surface by a special transporting system. But there are further problems. The coat would be subject to breaks and deformations as the cell changed shape during cell division or when moving or because of Brownian motion caused by the impact of fast moving atoms and molecules on the membrane surface. To keep it in order would require continual “surveillance” and repair mechanisms to stop gaps as soon as they occurred, to prevent the cell’s materials leaking out with potentially disastrous effects. The continual surveillance would necessitate various feedback systems to inform the cell of the state of the membrane. Even after adding more and more complex additional regulatory devices to our artificial membrane we would still be left with a very poor copy of the wonderfully fluid and motile self-assembling lipid bilayer membrane. And all this just to specify the cell membrane, let alone the myriads of different membrane structures all of which are based on the same basic bilayer design.

These thought experiments indicate the huge advantages that accrue to the cell by the use of natural self-organizing forms. What the membrane does is outperform any conceivable mechanical alternative and the cell gains its “coat” without the need for genetic specification, without the need for any assembling device, and without the need for complex regulatory circuits to sensor it for errors and breaks and initiate repair algorithms.

The exploitation of self-organization to assemble the spindle apparatus is also hugely advantageous for the cell. Being self-organizing, the spindle apparatus is a device that reaches its native form unerringly every single time on trillions of occasions throughout the life history of an organism. Like the cell membrane and a protein fold, it can assemble itself from all sorts of starting states and invariably and robustly arrive at the same structure, which pulls apart the two pairs of chromosomes at each cell division (Kirschner and Mitchinson 1986; Nedelec et al. 1997; Surrey et al. 2001). It is very difficult to see how the cell could successfully divide its genetic complement accurately at every cell division, except by using some sort of robust error free self-assembling structure.

Being self-organized structures, the nests of social insects also exhibit self-formative robustness. Like the folding of a protein or the formation of the spindle apparatus, the nests are constructed from all manner of starting states and via a myriad of different micropaths and like other self-organizing systems, the constructional process is robust in the face of all manner of perturbations. As Camazine et al., comment (2001: 338): “Robust self-repair is a common feature of self-organization.” To repair a self-organized pattern there is no need to invoke new and additional processes. As they continue: “the same self-organization process that built the initial pattern can operate to repair the pattern.” It is hard to see how insects would be able to construct engineering wonders such as the nests of tropical termites (Camazine et al. 2001: ch. 18) if they had to follow a detailed blueprint and had to apply all manner of complex repair algorithms.

In addition to their self-formative robustness, another major advantage of self-organization is that its genetic cost is minimal. Self-organization allows living systems (Camazine et al. 2001: 491): “to create complexity from simplicity with remarkable economy.” This means (Camazine et al. 2001: 89): “The richness of structure in nature does not depend or require a comparable richness in the genome...self-organization allows tremendous economy in the amount of genetic information that natural selection needs to encode in the genome.” Self-organization does not require a central control system, and detailed program, blueprint, recipe or template but arises through interactions internal to the system.

Finally, because self-organized systems lend themselves to sudden transitions between different emergent forms on minor changes in parameters of the system (characteristics of the components of the system) many different adaptive ends can be reached at minimal cost. This confers great adaptive flexibility on self-organized systems and facilitates relatively sudden changes from one stable state to another. (Camazine et al. 2001: ch. 3). This is classically illustrated in the variety of microtubular forms that can be generated on minor changes in the concentration of the key components of the system (Nedelec et al. 1997; Misteli 2001; Surrey et al. 2001).

We believe that taken together these adaptive advantages—such as ridding the organism of the burden of detailed genetic specification, of the need for an assembler device to put the structure in place, of the need for continual surveillance and repair *algorithms* to maintain it in its adaptive form, and providing flexible systems which lend themselves to rapid adaptive transitions—strongly suggest that self-organization might be very widely exploited at all levels of the biological hierarchy.

Self-organization at every level

The great adaptive advantage of self-organizing systems discussed above suggests that self-organization might be utilized very widely to create complex forms; that the folding of a protein may indeed be as Monod (1972: 93) inferred merely a “microscopic image of the autonomous epigenetic development of the organism itself.”

Although most cases are not as thoroughly characterized as in the case of protein folds or microtubular forms, already it is clear that the epigenetic generation of emergent complexity during development via the self-organization of gene products in the absence of any detailed genetic specification or feedback control is playing a role in a great many developmental processes especially in early embryogenesis. As Solter and Knowles (1999) comment: “We tend to think that [development] is achieved by regulation of gene expression at the transcription level alone. However, there are periods in development when transcription *does not even take place*” [our emphasis]. A well-characterized case of cellular self-organization is the development of the parasol of the unicellular algae *Acetabularium* (Goodwin 1994). Many symmetry breaking processes which generate cell polarity (Bornens 1999; Van Oudenarden and Theriot 1999) and determine embryonic axes (Motosugi et al. 2005; Cherdantseva and Cherdantsev 2006) are also largely self-organizing. Much of embryonic development from the fertilization of the egg to gastrulation and the laying down of the basic body plans of the major phyla is the emergent outcome of local cell–cell interactions (Kalthoff 1996; Nijhout 1999) often of a strikingly biomechanical nature (Keller et al. 2003; Green et al. 2004), rather than the outcome of a plan imposed on the embryonic cells by direct genetic instruction. An intriguing

example of biomechanical self-organization arising from local cell–cell interactions is the formation of the anterior–posterior mesodermal band in vertebrate embryos, recently described by Green et al. (2004: 580) as “extraordinarily robust and resistant to radical perturbation.” The closure of the blastopore and elongation of the primitive gut during *Xenopus* gastrulation brought about by “hoop stresses” in the embryo, is another intriguing case of “local cell behavior” resulting in a “global morphogenetic result” (Keller et al. 2003: 185). Gould (2002: 627) captured the emerging picture when he claimed that “organisms are stuffed full of emergent features...What else is developmental biology but an attempt to elucidate such nonlinearities?”

Self-organization is also widely held to have played a role in the origin of life (Kauffman 1993; Weber 1998; Woolfson 2000: ch. 11; Morowitz, 2002) and in the origin of evolutionary novelties, including body plans (Goodwin 1994; Newman 1993, 1994) and segmentation patterns (Newman 1993; Salazar-Ciudad et al. 2001a). Newman (1993) comments: “multi-component segment-forming systems found in contemporary organisms (e.g., *Drosophila*) are the products of evolutionary recruitment of molecular cues such as homeobox gene products that increase the reliability and stability of metamer patterns originally templated by generic self-organizing properties of tissues.” More recent kinetic modeling studies seem to confirm this, revealing as Salazar-Ciudad et al. (2001b) note, a tendency for: “emergent genetic networks associated with self-organizing processes to be replaced ... [during evolution] with hierarchical networks.”

The number of well-characterized self-organizing systems is still small, as Camazine et al. (2001: 491) concede, and they confess much work still needs to be done. And of course the actual role of self-organization in the origin of life (Kauffman 1993) or in the evolutionary origin of metazoan body plans is speculative (Newman 1994). However, sufficient cases have been identified—and more are continually being elucidated—to raise the very real possibility that given its great adaptive advantages a good deal of development in biology will eventually be shown to exploit the freely given order arising out of a series of complex self-organizational processes, where each individual process resembles as Monod (1972) envisaged the folding of an individual protein.

We conclude that self-organization as defined by Camazine et al. (2001: 8; quoted above) is *likely* to be extensively exploited to generate robust adaptive biological complexity at every level, from the molecular to the organismic. Indeed we suspect that the self-organization of matter into complex emergent *adaptive forms*, in the absence of any detailed blueprint (or recipe), may not just be widely used by organisms to generate complexity, but may turn out to be one of the *defining characteristics* of biological systems and perhaps a necessary mechanism for the generation of great complexity in any type of self-replicating system we might call life.

Challenging Darwinism

While the various ensembles (**a*b*c*d**) that self-organize instantaneously into emergent forms may be *discovered* by natural selection during the course of evolution and functionally fine tuned for various specific adaptive purposes (as acknowledged by Ruse 2003: 248), they could not have been *created* bit-by-bit by

cumulative selection. Selection can find an ensemble with self-organizing properties by “chance” and modify its behavior to some degree—what Camazine et al. (2001: 32) call “parameter tuning”—but it cannot create its behavior in the first place. Darwin’s bold proposal that natural selection is the maker of life’s adaptive design is undermined with every new self-organizing system that is discovered. The evolutionary role of natural selection is reduced from *creative agency* to more of an *eliminative mechanism*—which was how selection was seen to operate by pre-Darwinian thinkers like Lamarck, Chambers, Buffon and Owen (Gale 1972; Gould 2002: 143).

The idea that the self-organizing systems of biology might form a special life generating hierarchy responsible for the core fabric of the biological world is admittedly quasi vitalist. It would mean that life is a special and unique phenomenon without any significant analogy in the total space of all possible material forms; that any where in the cosmos, life is bound to be fundamentally similar to life on earth and that the biosphere is not merely a particular contingent subset of self-organized forms drawn from a vast infinity of alternatives, as Monod (1972: 49) implied when he claimed: “the biosphere does not contain a predictable class of objects or events.” On the contrary the order of life would be *lawful*, emergent in the self-organizing properties of matter. The paths of evolution from the hemoglobin fold (Denton et al. 2002) to insect segmentation patterns (Newman 1993) would be built into nature and determined by the emergent properties of matter. Biology would have re-adopted the basic framework of pre-Darwinian thought. As Dennett (1995: 260) comments such a deterministic view of evolution would render “Darwinism ... defunct, incapable of explaining any of the apparent design in the biosphere. It would be as if you wrote a chess playing computer program that could play one game by rote and, *mirabile dictu*, it regularly won against all competition!” Such a view would make a “mockery of Darwinism.”

The ontological status of self-organizing systems

There is a very obvious way to falsify (Popper 1965) the proposition that the self-organizing hierarchy of biology is unique: by the manufacture of an artifactual hierarchy of self-organizing systems that can simulate or mimic the self-organizing abilities of biological systems such as proteins, microtubular forms, membranes, embryos, etc. The creation of such a novel set of synthetic self-organizing adaptive systems, analogous to those utilized in nature, would immediately refute the claim that self-organization is unique to biology.

Biological self-organizing systems are all made out of the same materials—the same biomatter (mainly proteins)—in the same aqueous environment and are consequently close together in complex material space. Even if self-organizing systems analogous to those of biology could be manufactured out of diverse materials they would not form a natural set that could be discovered by some type of natural evolutionary process. The claim of uniqueness for the biological self-organizing hierarchy resides not merely in the fact of self-organization per se, but in the clustering and interdependent relationships of a very remarkable set of self-organizing systems, all within evolutionary reach—exhibiting evolvability (Kirschner and Gerhard 1998)—so that the magic of self-organization is easy to come by. In effect, to refute the idea that the self-organizing systems of life represent a finite unique set,

it is necessary to *artificially synthesize a whole clustered set of interdependent self-organizing material systems, all composed of a particular type of matter.*

There is no doubt that many obvious and profound similarities between organisms and machines do exist (Monod 1972; Kitano 2002; Csete and Doyle 2002) and that some of the mechanisms of life have been simulated in artificial systems. But despite the many similarities and the enormous advances in technology that have occurred over the past half century, such as the reduction of machines to the microscopic and nano level (Drexler 1986), the development of the computer and the many simulations of biology in computers (Levy 1993), no *artificial* material system has ever been built which exhibits the *robust self-organizing ability* of biological self-organizing systems. Most of the examples of “self-organization” alluded to in recent technical reports such as those cited by Barth et al. (2005: 672) in their recent *Nature* review, are as the authors admit, more correctly termed “self-ordered” or “self-assembly” and result in structures vastly simpler than those observed in biological systems. We agree with Brooks (2001) when he conceded recently that to date no artificial life form exists “which could be confused with a living organism for an instant.”

We believe that the failure to synthesize material forms mimicking the self-organizing systems of biology is a failure of enormous significance. The depth of this failure is obvious on casual perusal of the many very remarkable *in silico* simulations of biological patterns including, leaf like and shell like forms, shown by Wolfram (2002). The ease with which these can be simulated *in silico* alongside the failure to instruct matter to self-program into actual complex material forms is obvious and very suggestive. Despite the brilliance of human technology, despite our profound knowledge of chemistry and extraordinary ability to manipulate matter into what seems almost any conceivable complex supra-molecular form, and despite our ability to construct all sorts of highly sophisticated nano devices, to date no artificial self-organizing system has been designed that generates global complexity spontaneously from *local interactions among its component elements* remotely comparable with a protein, the spindle apparatus or a termites nest. None of the composite materials and complexes referred to in Yates et al. (1987) by Lehn (2002) by Whitesides and Grzybowski (2002) and Kurzweil (2005) is remotely comparable to a self-folding protein or a self-assembling spindle. Only *in silico*, in the realm of cellular automata (Langton 1989; Levy 1993; Wolfram 2002) are there examples of complex global forms or patterns—remotely comparable to the complexity generated in living things—emerging spontaneously out of the interactions between components of the system.

If it is the case as we suggest above, that exploiting self-organization is of *necessity* for complex material self-replication and if it is also the case that the self-organizing systems that are exploited by life are without analogy within the space of all material possibilities, then life as it exists on earth would be a unique phenomenon. This does have vitalist implications. However, we do not wish to conflate such a vitalism based on the uniqueness of life as a material phenomenon with traditional vitalism, like that of Driesch (1929), which presumed an indwelling soul or entelechy responsible for the self-organizing ability of organisms.

The pre-Darwinian hierarchy of self-organizing types

The idea that the forms of the organic world represent a unique finite set of natural and lawful forms was one of the grand unifying conceptions of

pre-Darwinian biology. One of the fundamental goals of biologists in the pre-Darwinian era was to uncover “the Laws of Biological Form,” which it was hoped would provide a rational and lawful explanation for biological form (Driesch 1929; Webster and Goodwin 1982; Gould 2002: ch. 4). Viewing organic forms to be natural types, determined by natural law like inorganic forms, the crystal became one of the most popular metaphors for organic form in the early 19th century. It was used widely by Carus, Theodore Schwann, Owen and Robert Chambers (Russell 1916). Schwann, the co-founder of the cell theory considered: “cytogenesis as a form of organic crystallization” (Rupke 1994). In the last chapter of his *Microscopical Researches* he draws extensive parallels between cells and crystals: “The process of crystallization in inorganic nature is the nearest analog 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” (Schwann 1847).

It followed from the conception of organic forms as lawful givens that the whole pattern of evolution was itself conceived of as pre-determined by natural law. In the concluding chapter of his *Anatomy of Vertebrates* Owen (1866) describes the path of evolution as “preordained...due to an innate tendency...by which nomogenously created [generated by law] protozoa have risen to the higher forms.” If biological forms were indeed the inevitable ends of natural law, life throughout the cosmos wherever it exists should be based on the same basic set of organic forms. This idea was clearly expressed by Chambers (1844) in *Vestiges*. Discussing life in the cosmos he comments: “Thus as one set of laws produced all the orbs and their motions and gnostic arrangements, so one set of laws overspread them with life.” And consequently: “the inhabitants of all other globes of space bear not only a general, but a particular resemblance to those of our own.” The same possibility was discussed by Owen (1849) in the concluding section of *On the Nature of Limbs* where he considers the possibility of the vertebrate body plan having been modified in different ways on different planets: “The laws of light as of gravitation being the same [on other planets]... the inference as to the possibility of the vertebrate type being the basis of organization of some of the inhabitants of other planets will not appear so hazardous.”

After the Darwinian revolution this naturalistic scheme was abandoned. Life and organisms were no longer seen as they had been in pre-Darwinian biology to be part of the *ocean of natural being*. Organic forms came to be seen increasingly as artifacts in essence, contingent, LEGO-like assemblages: put together bit-by-bit by selection during evolution and specified during evolutionary development from a detailed blueprint in the genes. After Darwin, organisms were reassigned from the realm of the crystal to that of the artifact (Denton et al. 2002). After August Weismann, because the specification of a contingent LEGO-like order required detailed genetic specification (pre-formation) rather than self-organization (epigenesis) the idea that all biological order is “in the genes” became the paradigm of biology and the 20th century became the century of the gene (Keller 2000). Self-specification replaced self-organization as the core paradigm of the biological sciences. Darwinism implied life’s order was contingent and the secret of life and the secret of form recurrence was in the genes, in self-specification not in natural self-organizing systems.

Although the modern term self-organization was not specifically applied by 19th century biologists to the basic types and archetypes of the living world the implication that types were natural self-organizing forms was implicit in the widely drawn parallel between organic types and crystals. And it is difficult to see what evolution by natural law (Chambers 1844) could mean other than the self-organization of matter. If the types are universals and bound to recur on different planets then this again implies that they arise deterministically from the self-organization of biomatter.

The pre-Darwinian conception of a special hierarchy of natural forms underlying the diversity of life and determining the major paths of evolution is consistent with the copious evidence for self-organization sited above. We find the parsimony and beauty of the idea that the basic forms of both the inorganic and the organic realms of nature may finally be shown to result from the same principle of self-organization immensely attractive and unifying.

Conclusion

We conclude that Darwinists like Weber and Depew (1996: 42) and Ruse (2003: 226–245) are wrong to suggest that self-organization can be easily accommodated with classic Darwinism, with its emphasis on cumulative selection as the sole maker of life's adaptive order. Of course self-organization does not *exclude* Darwinian selection or adaptive evolution. There is nothing in the nature of self-organizing systems that precludes their adaptive fine-tuning by selection. Indeed many self-organizing systems from protein folds (Denton et al. 2002), to insects' nests, lend themselves to adaptive fine-tuning (Camazine et al. 2001). However, self-organization is in the last analysis totally different in essence from cumulative selection as a causal agent of bio-complexity. If self-organization is in fact *widely exploited* by organisms to generate adaptive complexity, and we believe the evidence for this is rapidly accumulating, and if it has also played a crucial role in both the origin of life (Kauffman 1993; Weber 1998) and in the origination of body plans and phenomena like segmentation (Newman 1993, 1994), then this does indeed provide a serious challenge to the Darwinian claim that cumulative selection is the major *creative agency of evolution*. Self-organizing material patterns may be selected by, but *not created by natural selection*.

Moreover if the self-organizing systems turn out to be a unique material set built into the natural fabric of the world—and the evidence is to date entirely consistent with such an interpretation—then Darwinism is indeed profoundly challenged. For this would imply that the patterns of life are not contingent as Darwinists assert (Monod 1972; Gould 2002: ch. 12), but as pre-Darwinian biologists believed: necessary, or prefigured into the order of nature. Intriguingly, it seems the Darwinian claim that nature's forms are contingent and the main paths of evolution undirected by natural law will be tested over coming decades, not only by future advances in the biological sciences, but also by developments in fields outside of biology, such as supramolecular chemistry and nanotechnology. It is developments in these areas of advanced technology that may reveal over the next few decades the fundamental ontological status of biological self-organization and complexity, and whether or not life is unique.

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