

Self-Other Organization: Why Early Life did not Evolve through Natural Selection

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Abstract: The improbability of a spontaneously generated self-assembling molecule has suggested that life began with a set of simpler, collectively replicating elements, such as an enclosed autocatalytic set of polymers (or protocell). Since replication occurs without a self-assembly code, acquired characteristics are inherited. Moreover, there is no strict distinction between alive and dead; one can only infer that a protocell was alive if it replicates. These features of early life render natural selection inapplicable to the description of its change-of-state because they defy its underlying assumptions. Moreover, natural selection describes only randomly generated novelty; it cannot describe the emergence of form at the interface between organism and environment. Self-organization is also inadequate because it is restricted to interactions amongst parts; it too cannot account for context-driven change. A modified version of selection theory or self-organization would not work because the description of change-of-state through interaction with an incompletely specified context has a completely different mathematical structure, i.e. entails a non-Kolmogorovian probability model. It is proposed that the evolution of early life is appropriately described as lineage transformation through context-driven actualization of potential (CAP), with self-organized change-of-state being a special case of no contextual influence, and competitive exclusion of less fit individuals through a selection-like process possibly (but not necessarily) playing a secondary role. It is argued that natural selection played an important role in evolution only after genetically mediated replication was established.

Keywords: autocatalysis, acquired characteristics, natural selection, protocell, self-replicating automaton, origin of life

1. Introduction

This paper calls into question the assumption that early life evolved, like present-day life, through natural selection, and is rightly thought of and formally described in terms of ‘units of selection’. Since Darwin proposed the concept of natural selection, it has been thought that, in order to be applicable to the evolution of an entity, certain conditions must be met, such as (1) heritable random variation and (2) competition for scarce resources. Clearly life must exist and have replicated at least once before there can be variation and competition. So it is almost trivially true that natural selection cannot explain how the first (or second) animate entity came about. However, it is often assumed that once there were two or more, any ensuing adaptive change was due to natural selection. We will see that according to reasonable and widely accepted scenarios for how life began even this is unlikely, because natural selection further (3) prohibits inheritance of acquired characteristics (or at least requires that it be negligible compared to change due to differential replication of individuals with heritable variation competing for scarce resources). Moreover, even self-organization cannot describe the change-of-state that ensues when this condition is not met, because it is restricted to interactions amongst the parts of an entity; it cannot account for form that emerges at the interface between entity and environment.

The prohibition on inheritance of acquired characteristics is straightforward for present-day life, but not so for early life. The problem stems from the unlikelihood that early life replicated in a manner similar to present-day life, owing to the extreme improbability of a self-assembling molecule arising spontaneously. Recognition of this led to the well-known ‘chicken and egg’ problem: which came first, the nucleotides that make up a genetic self-assembly code which through transcription and translation leads to proteins, or the proteins that are necessary to many stages of the transcription/translation process? Many attempts to reconcile this paradox have been put forth (for an overview, see Fry 2000). Metabolism-first theories propose that the reducing atmosphere of early earth was conducive to the formation of a soup of organic molecules from amongst which the precursors of life arose (Haldane, 1929; Oparin, 1929/1936, 1957). Demonstration that amino acids could form spontaneously by an electrical discharge under conditions thought to simulate earth’s early atmosphere (Miller, 1953) led to a suggestion that life began with weakly catalytic proteins (Fox, 1988, 1993). Replication-first theories propose that life began with information carrying nucleotides or template-replicating polymers that together constitute a primitive genetic code (e.g. Crick, 1968; Gilbert, 1986; Lifson, 1997; Lifson and Lifson, 1999; Orgel, 1992, 1995; Maynard-Smith and Szathmáry, 1995). Other approaches can be considered a blend of metabolism-first and replication-first approaches (de Duve, 1995; Dyson, 1982, 1999; Eigen, 1971, 1992).

Still other theories, which may be referred to as ‘self-organization’ theories, suggest that life began with a chemically isolated, self-organized set of simple collectively replicating polymers,

and genetically mediated replication came afterward (Deacon, submitted; Kauffman, 1986, 1993, 1995, 2000; Morowitz, 1992; Wächtershäuser, 1992; Weber, 1998, 2000; Williams and Frausto da Silva, 1999, 2002, 2003). It is this theory of the origin of life that is presupposed in what follows. For simplicity, the process by which one organism generates another will be referred to as coded replication when it is genetically mediated, and uncoded replication when it is not [1]. Enclosed life forms that replicate through an uncoded, self-organized process are referred to as protocells.

We begin by examining how the assumptions underlying natural selection are incompatible with characteristics of protocells. We will look at a means of conceptualizing the evolution of early life that is consistent with reasonable scenarios for how life began and current theories of change-of-state. Specifically, it will be proposed that early life evolved through a process of self-other organization^{3/4}the emergence of form not just internal to an entity but at the interface between entity and context^{3/4}which is described as an interleaving of self-organization and context-driven actualization of potential, or CAP (Gabora and Aerts, 2005).

2. The Problem of Inheritance of Acquired Characteristics

In this section we examine the difference between coded and uncoded replication, and why inheritance of acquired characteristics is a consequence of the second but not the first.

2.1 Coded versus Uncoded Replication

Analysis of the formal requirements for self-replication led von Neumann (1966) to conclude that a self-replicating automaton (sometimes referred to as a replicator) consists of coded information that gets used in two distinct ways. The first way is as a set of self-assembly instructions that are actively deciphered to construct a replicant. In this case, the code functions as interpreted information. The second way is as a self-description that is passively copied to the next replicant. In this case, the code functions as uninterpreted information. There are of course deviations from this in present-day life, viruses being an oft-cited example. However these deviations can be accommodated within a Darwinian framework. Investigations into the question of how life began have quite naturally focused largely on the question of how such self-assembly instructions could have arisen spontaneously in the atmosphere of early earth. However, investigations of the possible relevance of connectivity and threshold phenomena in random graphs (Cohen, 1988; Erdős and Rényi, 1960) suggested an alternative possibility: that life arose without explicit template replication through autocatalytic closure of simple catalytic molecules (Bollobas, 2001; Bollobas and Rasmussen, 1989; Dyson, 1982, 1985; Kauffman 1986, 1993). In Kauffman's model, polymers catalyze reactions that generate other polymers, increasing their joint complexity, until together as a whole they form something that can more or less replicate itself [2]. The reason this works is that when polymers interact, the number of different polymers increases exponentially, but the number of reactions by which they can interconvert increases

faster than their total number. Thus, as their diversity increases, so does the probability that some subset of the total reaches a critical threshold where there is a catalytic pathway to every member. The set is autocatalytically closed because although no polymer catalyzes its own replication, each catalyzes the replication of another member of the set. So long as each polymer is getting duplicated somewhere in the set, eventually multiple copies of all polymers exist. At least some subset of the polymers spontaneously adhere to one another, forming a spherical vesicle such as a coascervate (Oparin, 1957), microsome (Fox and Dose, 1977; Fox, 1988), or liposome (Hargreaves et al. 1977; Deamer and Barchfeld, 1982) that encloses the polymer set (see also Deacon, submitted). Such a structure is prone to fission or budding, where part of the vesicle pinches off and it divides in two. Replication is far from perfect, thus ‘offspring’ are unlikely to be identical to ‘parent’. But so long as there is at least one copy of each polymer in each of the two resulting vesicles, they can self-replicate, and continue to do so indefinitely, or until their structure changes drastically enough that self-replication capacity breaks down. Thus we have two kinds of replicators (Gabora, 2004). Coded replicators such as present-day organisms use self-assembly instructions as proposed by von Neumann. This ensures they replicate with high fidelity, and acquired characteristics are not inherited. Replication-first theories assume that the earliest forms of life were of this kind. The second, uncoded replicators employ a self-organized autocatalytic process. Some form of uncoded replication is assumed by theories of the origin of life that do not start with template-replicating polymers, such as the autocatalytic model discussed here.

2.2 Uncoded Replication Results in Inheritance of Acquired Characteristics

A criticism of Kauffman’s origin of life scenario is that it lacks a means of generating heritable variation, and thus a mechanism for evolution (Lifson, 1997; Maynard-Smith and Szathmari, 1995). But as we have seen, because there is nothing to prohibit inheritance of acquired characteristics, the ‘usual’ impediments to the generation of novel variation do not exist. Since protocell replication is accomplished through an autocatalytic process rather than decoding of a genetic template, change accumulated over the course of a lifetime is not wiped out at the end of each generation but drawn into the lineage. Different chance encounters of polymers, or differences in their relative concentrations, or the appearance of new polymers, could all result in different polymers catalyzing a given reaction, which in turn alters the set of reactions to be catalyzed. The accumulation of acquired change can be to the extent that by the time the protocell divides it may already have changed dramatically. Thus the ‘replicant’ daughter cell can have quite a different dynamical structure from that of the parent protocell at the time of its own conception. This is sometimes referred to as Lamarckian evolution, though strict interpretations of the concept additionally require that the traits in question be acquired at the phenotypic level and subsequently modify the genotype to become heritable (e.g. Hull et al. 2001) [3]. This is clearly not the case here, for there is no clear genotype/phenotype distinction.

Specifically, since replication is not template-driven, there is no portion of the protocell that is (like a genome) shielded from contextually driven (environmentally accrued) change. And there is no portion of the protocell that is (like a body) shed at the end of the generation. A change to one polymer or replacement of one by another would be retained in at least one of the two daughter cells after fission, and this could cause other changes that have a significant effect on the lineage further downstream. It was not until the advent of explicit self-assembly instructions that acquired characteristics were no longer passed on to the next generation. From that point on, the only contextual interactions that exert much of an effect are those that affect the generation of offspring. Kauffman suggests that the uncoded-to-coded transition began with the chance evolution of polymers with a tendency to attach small molecules such as amino acids to their surfaces. Given their exterior location, these amino acids interact more with the environment than the polymers housed inside. This set the stage for a division of labor between the proteins that interact with the environment, and the nucleic acids concerned with replication. As Weber (2000) notes, any chemical change that increases capacity to remember information that enhances autocatalytic activity by encoding it in the polymers of nucleic acids, constitutes a step toward what we now think of as the genetic code. This is of course significant, in part because it enables information processes to be carried out recursively, and with greater precision, causing replication to become more constrained, robust, and shielded from external influence. From this point onward, acquired change only affected the lineage if it impacted the generation and survival of progeny (such as by affecting the capacity to attract mates, or engage in parental care).

2.3 Natural Selection Cannot Account for Inheritance of Acquired Characteristics

In present-day life, the prohibition on inheritance of acquired characteristics means that change accrued over the lifetime of an individual is not drawn into that individual's lineage but obliterated at the end of each generation. Thus it doesn't enter into the long-term picture, and we can afford to ignore it. Therefore, while for present-day life it is possible to describe the evolution process without a means of describing form that actualizes at the interface between entity and context, for protocells this is not the case. Acquired change occurs through the sculpting of existing structure rather than through selection of competing alternative structures. In other words, protocells get transformed and need not get selected amongst. Thus change is often occurring not through selection amongst individuals in a population of physically realized entities but through potential variations of a single entity.

Selection theory is inappropriate for the description of this kind of change of state. It can describe variation in a population of organisms, but not potential variations of one organism. More generally, when the entity of interest is a set of multiple physically realized or actual (as opposed to potential) sub-entities from amongst which some subset is selected, this is a deterministic process which can be described by a classical probability theory such as the

mathematical theory of selection developed by Fisher (1930), Haldane (1932), Wright (1931) and other population geneticists. Selection theory is concerned only with factors internal to the population, so nondeterminism in our model reflects a lack of knowledge of the state of the entity (the entity being not any one particular organism but the population). Nondeterminism that arises through lack of knowledge concerning the state of the entity can be described by classical stochastic models (e.g. Markov processes) because the probability structure is Kolmogorovian [4].

However, when change occurs not through selection amongst alternatives but through actualization of potential through interaction with a context, nondeterminism arises through lack of knowledge concerning the interaction between the entity and the context. It has been proven that this introduces a non-Kolmogorovian probability model on the state space, thus Bayes' formula for conditional probability is not satisfied (Pitowski, 1989). A Kolmogorovian probability model such as is used in population genetics, cannot be used (Accardi and Fedullo, 1982; Aerts, 1986; Aerts and Aerts, 1997; Piron, 1976; Randall and Foulis, 1976). Because the entity has the potential to change to many different states (given the various possible contexts it could encounter), we can say that it is in a potentiality state with respect to context. The mathematical description of change-of-state of an entity that is in a state of potentiality (where, given different contexts it would achieve different forms) is considerably more difficult than that of a population of already actualized (physically existing) entities whose change-of-state is taking place through natural selection. A fundamentally different kind of mathematical structure is required. It is only possible to ignore the problem of incomplete knowledge of context if all contexts are equally likely, or if context has a temporary or limited effect.

Potentiality and contextuality both stem from the fact that we inevitably have incomplete knowledge of the universe in which an entity is operating. We proceed as if a process can be isolated from its context and as if there could exist a class of processes which are identical, though it is obvious that any process and its context when considered in complete detail is a unique event. When the state of the entity of interest and/or context are in constant flux, or undergoing change at a resolution below that which we can detect but nevertheless affect what emerges at the entity-context interface, this gives rise in a natural way to nondeterministic change. In reality the universe is so complex we can never describe with complete certainty and accuracy the context to which an entity is exposed, and how it interacts with the entity. There is always some possibility of even very unlikely outcomes. However, there are situations in which we can predict the values of relevant variables with sufficient accuracy that we may consider the entity to be in a particular state, and other situations in which there is enough uncertainty to necessitate the concept of potentiality. Thus a model of the evolution of an entity must ordinarily take into account the degree of knowledge we as observers have about the context. But because in the modern-day evolution of biological form acquired traits are not heritable, we can get away with a model that does not incorporate the effect of context.

3. The Problem of Inconclusive ‘Death’

Another assumption of selection theory is that individuals are lost from the population and replaced by new ones, giving rise to discreet or overlapping generations. The notion of generation is sometimes construed in more abstract treatments as iteration (e.g. Holland, 1975; Hull et al., 2001). Mathematical analyses of selection processes are predicated on the ability to state up front whether particular individuals do or do not constitute members of a given generation or iteration.

However, ‘death’ of a protocell goes unnoticed; concretely there is not much to distinguish a ‘dead’ protocell from a ‘living’ one except one continues to spawn replicants and the other doesn’t. Indeed we must wait until after the fact of its replication to determine that it was ‘alive’ prior to the replication event. A seemingly dead protocell could ‘come back to life’ when the circumstances for its replication became right. Because there is no hard and fast distinction between a living individual and a dead one, there is no definitive basis for determining what constitutes a generation.

4. The Limitations of Self-Organization

The success of self-organized autocatalysis as an explanation for the origin of life might appear to suggest that self-organization can take over where natural selection leaves off and together they provide a complete explanation of the origin and evolution of living things. Indeed, to the extent that the state of a protocell at a particular point in time reflects its composition of polymers and their internal pattern of catalysis, its dynamics can be described by recourse to self-organization. However, to the extent that the protocell’s state reflects interaction that takes place between it and its environment, natural selection and self-organization are both insufficient. Self-organization can explain how parts reorganize to give rise to an entity that may have properties that were not present in the parts. But it is still limited to the entity and its parts. It cannot describe change that occurs due to the potentiality to actualize new form through interaction with different contexts that could be encountered.

5. Context-driven Actualization of Potential (CAP)

In this section we review a general scheme for change of state of an entity under the influence of a context (Gabora and Aerts, 2005). In the section that follows we will examine its implications for the origin of life.

Since we do not always have perfect knowledge of the state of the entity, the context, and the interaction between them, a general description of an evolutionary process must be able to cope with nondeterminism. Evolutionary systems differ with respect to the degree of determinism involved in the changes of state that the entity undergoes. Consider an entity in a state $p(t_i)$ at an instant of time t_i . If it is under the influence of a context $e(t_i)$, and we know with certainty that $p(t_i)$ changes to state $p(t_{i+1})$ at time t_{i+1} , we refer to the change of state as deterministic.

Newtonian physics provides the classic example of deterministic change of state. Knowing the speed and position of a ball, one can predict its speed and position at some time in the future. In many situations, however, an entity in a state $p(t_i)$ at time t_i under the influence of a context $e(t_i)$ may change to any state in the set $\{p_1(t_{i+1}), p_2(t_{i+1}), \dots, p_n(t_{i+1}), \dots\}$. When more than one change of state is possible, the process is nondeterministic.

5.1 Nondeterminism with respect to State of Entity

Nondeterministic change can be divided into two kinds. In the first, the nondeterminism originates from a lack of knowledge concerning the state of the entity $p(t_i)$ itself. This means that deep down the change is deterministic, but since we lack knowledge about what happens at this deeper level, and since we want to make a model of what we know, the model we make is nondeterministic. This kind of nondeterminism is modeled by a stochastic theory that makes use of a probability structure that satisfies Kolmogorov's axioms.

5.2 Nondeterminism with respect to Context

Another possibility is that nondeterminism arises through lack of knowledge concerning the context $e(t_i)$, or how the context interacts with the entity of interest [5]. This is where the notion of potentiality state introduced in section 3 becomes useful. It must be stressed that a potentiality state is not predetermined, just waiting for its time to come along, at least not insofar as our models can discern, possibly because we cannot precisely specify the context that will come along and actualize it. Note also that a state is only a potentiality state in relation to a certain (incompletely specified) context. It is possible for a state to be a potentiality state with respect to one context, and a deterministic state with respect to another. More precisely, a state that is deterministic with respect to a context can be considered a limit case of a potentiality state, with zero potentiality.

5.3 A Formalism that Describes Both

We have seen that the description of the evolutionary trajectory of an entity may involve nondeterminism with respect to the state of the entity, the context, or how they interact. An important step toward the development of a complete theory of evolution is to find a mathematical structure that can incorporate all these possibilities. There exists an elaborate mathematical framework for describing the change and actualization of potentiality through contextual interaction that was developed for quantum mechanics. However it has several limitations, including the linearity of the Hilbert space, and the fact that one can only describe the extreme case where change of state is maximally contextual. Other mathematical theories lift the quantum formalism out of these structural limitations, making it possible to describe nondeterministic effects of context in other domains (Aerts 1993; Aerts and Durt 1994; Foulis and Randall 1981; Foulis et al. 1983; Jauch 1968; Mackey 1963; Piron 1976, 1989, 1990; Pitowsky 1989; Randall and Foulis 1976, 1978). Although the original motivation for these

generalized formalisms was theoretical (as opposed to the need to describe the reality revealed by experiments), they have now been applied to macro-level as well as micro-level situations with varying degrees of contextuality (Aerts, 1982, 1991; Aerts et al., 2000). In fact, classical and quantum come out as special cases: quantum at one extreme of complete contextuality, and classical at the other extreme, complete lack of contextuality (Aerts, 1983; Piron, 1976). These formalisms can be applied to evolution processes, which differ according to not just the degree of contextuality but also according to the degree of internalization of and dependency upon context, as well as whether nondeterminism, if present, is due to lack of knowledge concerning the state of the entity or lack of knowledge concerning the state of the context (Gabora and Aerts, 2005).

6. Evolution of the Protocell through Self-Other Organization

Both coded and uncoded replicators evolve by actualizing potential that exists due to the state of the entity, the context, and the nature of their interaction. For modern-day life, context-driven change at the level of the individual is lost from the lineage, so natural selection, a less direct, population-level means of change, becomes significant. But because protocell replication occurs not according to instructions, but through happenstance interactions, context-driven change is retained. There is no a priori reason such a process has to be Darwinian or involve selection. To the extent that the different possible contexts a protocell could encounter would give rise to a different interaction dynamics, the description of this change of state requires a nonclassical probability model. We may refer to emergence of form that results through this interaction between self and context as self-other organization to distinguish it from form that emerges through interaction amongst the parts of an entity. Self-other organization is not a competing explanation to self-organization. They work in concert; novelty generated through self-other organization at the interface between entity and context propagates through the entity to bring about self-organized change from within.

Let us now consider a scheme for describing context-driven evolution of a protocell. Let us say a protocell undergoes a change of state from $p_0(t_0)$ to $p_4(t_1)$. The change of state of the protocell may evoke a change in its environment or context. Alternatively, the context may change of its own accord, or the ensuing self-organization may change the sort of context it is subsequently susceptible to. Under the influence of this (possibly altered) context, which we call $e(t_1)$, there may be many potential states it could change to. We denote this set of states $\{p_1(t_2), p_2(t_2), \dots, p_n(t_2), \dots\}$. At time t_2 , one of these states, for example $p_3(t_2)$, may actualize. And so forth, recursively. The states $p(t_0), p(t_1), p(t_2), \dots, p(t_i), \dots$ constitute the trajectory of the protocell through state space, and describe its evolution in time. Thus, the evolution of a protocell is described as incremental change resulting from recursive, context-driven actualization of potential, or CAP. This process may consist of both deterministic and nondeterministic segments. In deterministic segments, the protocell changes state in a way that follows predictably given its previous state and/or the context to which it is exposed, and this can be described as a

process of self- organization. In nondeterministic segments this is not the case; self-other organization is needed. Clearly, the transition from uncoded to coded replication, while ensuring fidelity of replication, decreased long-term sensitivity to and internalization of context, and thus capacity for context independence. Thereafter until the advent of sexual replication, one generation was almost identical to the next, and the evolution process became more deterministic. With the advent of sexual reproduction, the contextuality of biological evolution increased. Consider an organism that is heterozygous for trait X with two alleles A and a. The potential of this Aa organism gets actualized differently depending on the context provided by the genotype of the organism's mate. In the context of an AA mate, the Aa organism's potential is constrained to include only AA or Aa offspring. In the context of an aa mate, it has the potential for Aa or aa offspring, and once again some of this potential might get actualized. And so forth. But while the mate constrains the organism's potential, the mate is necessary to actualize some of this potential in the form of offspring. In other words, the genome of the mate simultaneously makes some aspects of the Aa organism's potentiality possible, and others impossible. An organism exists in a state of potentiality with respect to the different offspring (variants of itself) it could produce with a particular mate. In other words, a mate constitutes a context for which an organism is in a state of potentiality. One can get away with ignoring this to the extent that one can assume that mating is random. Note that since a species is delineated according to the capacity of individuals to mate with one another, speciation can be viewed as the situation wherein one variant no longer has the potential to create a context for the other for which its state is a potentiality state with respect to offspring. A species can be said to be adapted to the extent that its previous states could have collapsed to different outcomes in different contexts, and thus to the extent that its form reflects the particular contexts to which it was exposed. Note also that although over time species become increasingly context dependent, collectively they are becoming more context independent. (For virtually any ecological niche there exists some branch of life that can cope with it.)

7. Summary and Conclusions

It is often assumed that if an entity constitutes a unit of evolution it follows automatically that it constitutes a unit of selection. But there is no reason evolution need involve selection, except as a special case. The assumptions of natural selection---including coded replication, successive generations, and negligible inheritance of acquired characteristics---are natural and non-problematic in considerations of modern-day prokaryotes and eukaryotes. However they are unnatural and problematic in considerations of life prior to genetically mediated protein synthesis. We are so used to thinking in terms of competition amongst individuals with genomes and fixed lifespans that it may have warped our ability to think clearly about entities without fixed lifespans, that replicate without genomes. Their challenge may be not so much to out-compete neighbors as to enhance ones' own energetic efficiency enough to maintain and

replicate a ‘proto-metabolism’ (irregardless of how well neighbors are doing).

In fact the problem with applying natural selection to protocells is not merely that it would be possible for a protocell to evolve^{3/4}undergo adaptive descent with modification^{3/4}without selection. The problem is more acute: the assumptions that render natural selection applicable to the description of genetically mediated life do not hold for protocells. Protocells do not engage in template replication; their replication proceeds without a code through a self-organized autocatalytic process. As a result, there is no definitive distinction between dead and alive, and more importantly, since replication is not code-driven, acquired characteristics are inherited. A modified version of selection theory or self-organization would not work because the description of change-of-state through interaction with an incompletely specified context has a completely different mathematical structure, i.e. entails a non-Kolmogorovian probability model. It is possible to ignore this effect of context if all contexts are equally likely, or if context has a limited effect on heritability. Context does have a limited effect on heritability for code-mediated forms of life, but not for uncoded forms of life such as protocells, which replicate through a self-organized autocatalytic process. Neither is the addition of self-organization to a theory of evolution sufficient to complete the picture, because it is restricted to explanation of change that occurs through interactions amongst parts rather than interaction with a context.

It is proposed that the evolution of early life occurred not through competitive exclusion of less fit individuals through natural selection but through transformation of lineages through context-driven actualization of potential, or CAP. Specifically:

- An entity has the potential to change in different ways under different contexts. Some aspects of this potentiality are actualized when the entity undergoes a change of state through
- interaction with the particular context it encounters. The interaction between entity and context may also change the context, and the constraints and
- affordances it offers the entity.

Thus the entity undergoes another change of state, and so forth, recursively. Different evolutionary processes vary with respect to the degree of indeterminism due to context, the degree of context independence, and the degree to which context-driven change is retained in future lineage(s). This move constitutes a crucial step toward incorporating ‘relation’ into our theories of living things (Rosen 1991). Almost every entity changes through this simpler means of contextual interaction, not only physical entities, but also cultural artifacts (Gabora 2004; Gabora and Aerts 2005) and ideas as they are being honed in a stream of thought (Gabora 2005). This paper has argued that natural selection becomes salient in the evolution of a lineage only after a self-replication code (e.g. genetic code) has been established. Only once change accrued through contextual interaction starts to get wiped out at the end of each generation can selection start to play a dominant role in evolution. It is somewhat ironic that though the term ‘adaptation’

is most closely associated with biology, biological form is in fact exceptionally resistant to internalization and retention of context-driven change. This explains why it has been possible to develop a theory of biological evolution that all but ignores the problem of incomplete knowledge of context.

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[1] Dyson (1985) reserves the term ‘replicator’ for coded replicators, and uses the term ‘reproducer’ for uncoded replicators. However, this terminology is potentially confusing given that elsewhere (e.g. Szathmáry & Maynard Smith 1997) the term ‘reproducer’ is associated with sexual reproduction. The distinction between coded and uncoded replicators is related, but not identical to, Szathmáry and Maynard Smith’s (1997) distinction between modular and processive replicators.

[2] Kauffman’s proposal for how life began has been criticized for its strict mathematical

assumptions such as binary sequences (only two amino acids) and each molecule had the same fixed probability of catalyzing a given reaction (Joyce 1989; Lifson 1997; Maynard-Smith & Szathmary 1995), though conditions under which autocatalysis occurs with under looser sets of assumptions have been delineated (Hordijk & Steel 2004; Mossel & Steel 2005; Steel 2000).

[3] Since the existence of the genotype was not known at the time the notion was proposed by Lamarck, this strict interpretation of the concept is surely not what he had in mind. This is why it is the looser use of the term that is adopted here; thus any means by which acquired traits are inherited counts as Lamarckian.

[4] Kolmogorov (1933) formulated the axiomatic system for classical probability theory. Thus a classical probability theory is one that satisfies Kolmogorov's axioms (i.e. a Kolmogorovian probability theory). An example of a domain in which Kolmogorov's axioms are not satisfied is quantum mechanics (Wilce, 2003).

[5] Yet another possibility is that the nondeterminism is ontological i.e. the universe is intrinsically nondeterministic at bottom. In this case, it can be shown that the mathematical structure necessary to model the situation is equivalent to the mathematical structure needed to model the situation where the nondeterminism arose through lack of knowledge of the context, i.e. the probability model needed also does not satisfy Kolmogorov's axioms (Aerts, 1994). Thus, ontological indeterminism can also be described in this framework.