Let There Be Life

Thermodynamic Reflections on Biogenesis and Evolution

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The question of how life emerged from inanimate matter is closely related to the more fundamental question, namely: What is life? Both issues yield novel insights when discussed in the light of thermodynamics. The model proposed here is based on a simple assumption, namely, that life began with the accidental assembly of a self-replicating molecule. From this assumption the emergence of life naturally follows, enabling a new understanding of evolution as a whole. The evolution of any type of self-replicating systems, even the simplest ones, is shown to be highly efficient in extracting, recording and processing information about the environment. A variety of related issues yield some surprising conclusions when discussed in the thermodynamic context. New processes of order-increase are pointed out, a novel measure of information is proposed, and Lamarckianism is proved to be inconsistent with thermodynamics. Recent works on biogenesis and evolution are critically reviewed.

1. Life's Origin and Nature: Two Related Riddles

Darwin's (1859) theory of evolution has secured a unique position in the history of science owing to its spectacular explanatory power. It addressed an age-old riddle. Adaptation, in countless ingenious forms, is the universal hallmark of life. This trait seems to defy ordinary notions of causal order, since every newborn organism is endowed with *inborn* means of coping with specific environmental menaces that will face it *later*. Whence these inborn ingenuities and how do they succeed to anticipate needs not yet existent?

Evolutionary theory purports to explain this plethora of biological wonders on the basis of only three arguments, based on simple observations. The first argument simply states: (i) "Living organisms beget similar offsprints." The second restricts the first by adding that, nevertheless, (ii) "Offsprings of the same parents often differ from one another." The third can be bluntly put as (iii) "Life is tough; only few offsprings reach maturity." In the Darwinian framework, these three common-sense statements

alone suffice to derive the entire billions-year drama of life on Earth. They can, in principle, explain how any form of biological adaptation has evolved. It is this ratio of few arguments "invested" to many explanations "gained" that grants the theory its strong heuristic power.

Yet, any evolutionist resolution of a biological question only highlights the most intriguing riddle: How did all this begin? As one envisages separate lineages of organisms converging pastwards into common origins, one inevitably feels curious about the ultimate convergence point, the first event of "biogenesis" that marked the beginning of all life on Earth. Indeed, biochemistry points out some features common to all known living forms. They all possess the same genetic code. More intriguing, all their proteins are composed of "left-handed" amino acids, while their nucleic acids (DNA and RNA) are made of "right-handed" sugars. This is unusual, bearing in mind that, from the purely physical viewpoint, all interactions (save those associated with the weak force) are perfectly symmetric in space (Elitzur, 1993*b*). Therefore there is no physical reason for

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these biological asymmetries; life could as well possess the mirror-images of the proteins and nucleic acids (as well as the reverse physiological asymmetries) and still all biological processes would be exactly the same. The evolutionary explanation for this handedness is simple: It was a common ancestor that, by sheer coincidence, happened to have these molecules rather than their mirror-images (Shapiro, 1986; this issue will be returned to later). This coincidental yet universal handedness of life highlights the question of common ancestry, vividly raised by Darwin:

> But if (and oh! what a big if!) we could conceive in some warm little pond, with all sorts of ammonia and phosphoric salts, light, heat, electricity, etc., present, that a protein compound was chemically formed ready to undergo still more complex changes, at the present day such matter would be instantly devoured, or absorbed, which would not have been the case before living creatures were formed. (Quoted in Mayr, 1982, p. 582.)

In this paper this "big if" will be addressed in detail. Such an undertaking promises much more than just a scenario of life's beginning; seeking a physical process that gave rise to evolution ought to shed new light on evolution and life in themselves.

Is such a task realistic? Apparently, it requires a great deal of data, mostly unavailable at present, about the conditions that prevailed on Earth before the emergence of life. But this is not necessarily so. More elementary work on the theoretical level is first warranted, regardless of specific chemical and physical details. The model should, as long as possible, avoid assuming any law of Nature other than those given by physics.† One does not necessarily commit oneself to "reductionism", "physicalism" or any other "ism" if one believes in a profound unity of all natural sciences, a unity that enables biology to be placed on the solid foundations of physics. In this framework, evolutionary theory demonstrates its best explanatory power. The laws of physics would then be the sole "input" for a simple and parsimonious theory that, like Darwinism in general, yields a plenitude of explanatory "output" in return.

2. Thermodynamics as a Unifying Paradigm: Adaptation, Order and Information

The above-stated approach makes thermodynamics the most suitable branch of physics for our task. Thermodynamics is a substance-independent theory, i.e. its laws apply to *all* physical systems, irrespectively of their structure, chemical constituents or specific form of energy. It therefore seems to provide the most

† "Physics" is used here in the broad sense, including chemistry.

promising prospects for a physical foundation for biology (Prigogine & Stengers, 1984; Wicken, 1985a, b). Many works, classical as well as recent (Schrödinger, 1945; Szent-Györgi, 1957; Gatlin, 1972; Lamprecht & Zotin, 1978; Morowitz, 1978; Babloyantz, 1991; Peliti, 1991) attest to this potential.

In fact, thermodynamics became relevant to biology as early as the time the former science was founded during the nineteenth century, when it was noticed that both disciplines deal with energy exchanges, irreversible processes and "order". The latter notion, though, has brought an apparent conflict between the two sciences, the resolution of which will be the aim in this article, but the very conflict makes the two realms even more relevant to one another.

Another concept that thermodynamics deals with, namely, information, makes this relevance to biology more subtle, as information underlies the very phenomenon of adaptation. Adaptation to an environment requires, first and foremost, information about it. A better understanding of evolution might therefore be gained by its study as an information-accumulating process.

The match between the two disciplines also involves a historical curiosity. Many pioneers of modern physics, such as Bohr and Wigner (see Volkenstein, 1991, for a brief review), argued that physics cannot provide a satisfactory basis for biology. This disbelief is echoed by biologists like Mayr (1982), who advocate the emancipation of biology from physics. Among the physicists who shared this view of physics's inadequacy to explain the phenomena of life were some notable pioneers of thermodynamics. Helmholtz (quoted in Zotin, 1978) argued that the Second Law does not always hold for biological phenomena. Lord Kelvin claimed that life transcends physical laws (see Brillouin, 1964; Leff & Rex, 1990c). Schrödinger (1945), in his classic *What is Life?*, has stated:

> We must therefore not be discouraged by the difficulty of interpreting life by the ordinary laws of physics. For that is just what is to be expected from the knowledge we have gained of the structure of living matter. We must be prepared to find a new type of physical law prevailing on it. Or are we to term it a non-physical, not to say super-physical law? (pp. 80–81)

His answer to the last question was negative, resorting somewhat vaguely to quantum mechanics as the source of the missing principle. He was therefore not confident that thermodynamics alone can provide the physical basis for biology. Similarly, Brillouin (1949) argued that thermodynamics remains incompatible with biology, leaving phenomena such as reproduction, maintenance of life, and free will

inexplicable (p. 99). Later, leaning towards a new version of Bergson's *élan vitale*, Brillouin (1964, p. 67) ventured to propose that some form of advanced waves (i.e. waves propagating in the past direction, in contrast to the normal form allowed by thermodynamics) may play a dominant role in biology. He concluded:

> We have been looking, up to now, for a physico-chemical interpretation of life. It may well happen that the discovery of new laws and of some new principles in biology could result in a broad redefinition of our present laws of physics and chemistry, and produce a complete change in point of view (p. 103).†

Ironically, it was both Schrödinger and Brillouin who have contributed some seminal insights that can make thermodynamics a universal basis for all living phenomena. As this paper intends to show, it is the Second Law of Thermodynamics itself that enables the most satisfactory explanation of evolution.

However, a caveat is advisable. Anyone who has glanced at the existing literature on this interface between thermodynamics and biology is familiar with the annoying semantic confusions and polemicism plaguing it (see review in Section 11). Aiming for clarity and simplicity, despite the complexities inherent to the subject matter, is yet another challenge awaiting us.

We will start with three thermodynamic concepts that will prove highly fruitful for our goals: "entropy", "order" and "information". What we need is some concise definitions, presented with the minimum of necessary mathematics, in order to efficiently apply them later to the problems awaiting us.

The Second Law of Thermodynamics, which has a somewhat unique position among the laws of physics (see Elitzur, 1992, 1994c), states that in any closed system there must be either a conservation or a increase of entropy. Consider the process shown in Fig. 1. After the slit has been opened, the gas spontaneously spreads over the box's two halves. Entropy is said to have increased in this process. What is entropy? There are several, partly overlapping, characterizations of entropy prevalent in the literature (see Gatlin, 1972). We will briefly review all of them.

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† Smith & Morowitz (1982) suggest that the missing additional law is "of the same epistemological character of the exclusion principle" (1949, p. 275).

‡ It has been realized long ago that thermodynamics requires Hell to be not only hot but isothermal as well. If there are even slight differences of temperature, the physicists and engineers living there can exploit the temperature differences for building refrigerators.
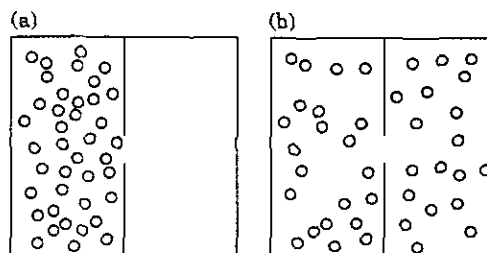

FIG. 1. Entropy increase manifested by gas reaching equilibrium.

(i) Entropy means equilibrium. The gas in Fig. 1 ends up being evenly distributed between the two halves.

(ii) Entropy is disorder. The final distribution of the gas molecules is clearly less ordered than the initial one. (This would have been more notable had there been two pure gases in the box's two halves: they would mix up.) Disorder, strictly defined, means that any constituent of the system has the same probability of being in all possible states. In our case, each molecule has equal probability of being in either part of the box.

(iii) Another manifestation of disorder and entropy is the independence of the states of the system's constituents. In our case, the position of each molecule is hardly affected by that of another one.

(iv) Entropy degrades the energy's efficiency during the latter's transformation from one form to another. In other words, "free energy", available for work, becomes "bound energy", i.e. hard to extract. Thus, kinetic and electromagnetic energies, that are the most efficient, transform into the less efficient chemical energy and finally (or even directly) into heat energy, useless for work (unless a *colder* body is introduced into the system, creating a new disequilibrium).‡ In the case considered in the figure, the kinetic energy that creates pressure on the dividing wall is eventually transformed into mere heat.

(v) Entropy-increase is irreversible. In the figure, the initial state can spontaneously evolve into the final one, not vice versa.

(vi) Entropy is a state of higher probability. The chance for a system to return to the initial, ordered state, while not zero, decreases rapidly with the number of the system's constituents. In our case, there is a very slim chance that so many molecules would return by themselves into the half from which they spread out.

(vii) Entropy is a macrostate compatible with more microstates than order. By "macrostate" we refer to the system's macroscopic values, such as heat and pressure, while "microstate" denote the system's microscopic arrangement, i.e. the positions and velocities of its molecules. When we see an ordered state,

we can infer its microstate with great certainty as there are only a few microstates compatible with it. A disordered state, in contrast, can stem from many microstates. In our case, there are numerous possible ways of arranging the molecules in the entropic stage, and much less in the ordered one. Everyday experience confirms that there are many forms of disorder but few ones of order.

Entropy-increase can be reversed, says the Second Law, only locally, and at the price of increasing the entropy elsewhere. For example, it is possible in principle to reverse the velocities of all the molecules in Fig. 1 so that, after a while, they will return by themselves to the half in which they were initially confined. However, the work needed for such a precise reversal of the molecules' motions requires energy that is proportionate to the required precision, and this energy's dispersal would increase entropy outside the system to a degree that would more than compensate for the local decrease of entropy inside. The Second Law always wins.

Having defined entropy and order, one can see how the concept of information is closely related. Information is a sequence of symbols that is highly correlated with a certain reality. The reality and the information describing it form an *ordered* relation, a state that is unlikely to be created by chance. Information is therefore the opposite of entropy. Indeed, the generation of information is subject to all the thermodynamic constraints imposed by the Second Law, as the information is bound to degenerate into random "noise", like other forms of order.

With the above thermodynamic notions in mind, the challenge posed to us by the phenomenon of life is clear. Life manifests striking exceptions to all the seven measures of entropy-growth reviewed above.

(i') The living state is the opposite of equilibrium; an organism reaches equilibrium with the environment only upon dying and decomposing. In fact, the higher the living organism is on the evolutionary tree, the more *autonomous* it is. The constancy of the organism's internal environment is a well-established measure of evolutionary level.

(ii') Life is a highly ordered phenomenon. It displays structures and operation modes that strictly follow unique patterns. A rose is a rose is a rose, because the shape and position of each of its leaves and petals are by no means random, neither are all the other constituents of any living organism.

(iii') Likewise, these constituents are highly dependent on one another. The symmetry of many animals is only one common example: One of the animal's side is nearly identical, in shape and form, to the other.

(iv') Life is capable of transforming low- to high-efficiency energies. Hatching eggs, for example, transform heat into chemical, electric and mechanical work even under isothermal conditions, as an insect's egg absorbing heat from the air.

(v') Life reverses otherwise-irreversible processes, creating ordered structures from disordered materials. This reversal is striking because it occurs not only on the microscopic scale; the organism imposes it on billions of molecules.

(vi') The living state is highly improbable. It is unthinkable that few chemical elements put together would spontaneously generate even the simplest biological structure.

(vii') The living state is compatible with a very few microstates. A healthy elephant's state is compatible with very exact and tiny amounts of iodine, insulin and adrenaline in its blood and even tinier amounts of other hormones and neurotransmitters. The living state's relation to its microstates is the very opposite of that of high entropy.

How can this thermodynamic contrast between animate and inanimate phenomena be accounted for? It has been realized long ago that the conflict is only apparent: the Second Law deals with closed systems whereas living organisms are open systems. That this general resolution is insufficient will become clear once we recall that nearly all the systems we see around us are open, yet they do not grow or evolve. To the extent that they exhibit local increases of order, this order is entirely different from the biological one. A "dissipative structure" or a "strange attractor", of the kind that chaos students are so fond of, do indeed display highly ordered patterns, self-generated or even self-maintained, yet they show *no adaptation* to the environment, *no information* is fed into them from the environment. It is these phenomena, so inherent to life, that pose the real challenge. Can thermodynamics enable us to understand them?

Here, recalling the other question, posed above, we shall make life harder (in both senses) by asking the two questions together. Thermodynamics can equip us with the appropriate conceptual tool to handle both. The question "How did life begin?" is closely related to the question "What is life?" and invites a fresh look into some of biology's most fascinating issues.

3. Basic Mathematical Definitions

The mathematical definitions of the above concepts have to be briefly dealt with before turning to the main theme of this paper.

Entropy is a function of the number of compatible microstates [definition (vii) above]. Boltzmann's equation expresses this relation thus:

$$S = k \ln W, \tag{1}$$

where k is Boltzmann's constant and W is the number of possible microstates. The more disordered a state is, the more ignorant it leaves us about its microstate. If the probability for any microstate is $p_i = 1/W$, then

$$S = -k \ln p_i. \tag{2}$$

This definition is good as long as all the different microstates have the same probability, which is the case only when they all have the same energy. In systems that exchange energy with their environment, the different microstates are not equiprobable, so a more general definition is needed:

$$S = -k \sum_{i=1}^{w} p_i \ln p_i, \tag{3}$$

where p_i is the probability for the i-th microstate.

This definition, as we have already noticed, seems to be good also for information. Entropy measures information's opposite, namely, *uncertainty*. This has led Shannon (Shannon & Weaver, 1963) to define the information of a message as the difference between the two uncertainties, the one from which one has initially suffered and the one after receiving the message. The initial uncertainty is defined exactly as entropy in eqn (3):

$$S(Q \mid X) = -k \, \Sigma \, p_i \ln p_i, \tag{4}$$

where Q is the question one asks about the system's state, X the knowledge about it, k is a constant and p_i is the probability of states $1, 2, \ldots, i$. The definition for information follows naturally:

$$I = S(Q \mid X) - S(Q \mid X'), \tag{5}$$

where X' is the new knowledge.

Brillouin (1956) has similarly defined information in terms of the initial uncertainty. Let there initially be P_0 possible states, all equally likely, so there is no initial information, $I_0 = 0$. Having received the information, the number of possibilities reduces to P_1. The information gained is

$$I_1 = K \ln(P_0/P_1) = K(\ln P_0 - \ln P_1). \tag{6}$$

Ideally, the information allows only one possible state, $P_1 = 1$, in which case eqn (6) reduces to

$$I_1 = K \ln P_0. \tag{7}$$

At first sight, it looks odd that this definition of information is identical with that of entropy in (1), but this would be easy to understand when we recall

that information is strictly proportionate to the initial uncertainty it has eliminated.

Shannon (Shannon & Weaver, 1963) has defined the information content of a single symbol out of a given set. In the case of the English alphabet, there are 27 letters (including the space sign), yet the probability for the occurrence of a letter is not equal to that of the others, hence the average information per letter is

$$i = -k \sum_{j=1}^{27} p_i \ln p_i. \tag{8}$$

So, in a sentence containing G symbols the information content will be

$$I = G \cdot i = -Gk \sum_{j=1}^{j=m} p_i \ln p_i. \tag{9}$$

Here again, information is defined similarly to entropy in (4). It is a function of the uncertainty (entropy) that would prevail in the information's absence. This relation is reflected also in more modern definitions that measure the order or information inherent in the system *itself*, regardless of any observer. Layzer (1978) defines information as the difference between the maximum entropy in which the system could be and the entropy in which it actually resides:

$$I = S_{\max} - S_{\text{act}}. \tag{10}$$

Likewise, Landsberg (1984; 1989) defined order as

$$Q = 1 - (S_{\text{act}}/S_{\max}). \tag{11}$$

A few comments are needed to conclude this brief introduction to thermodynamics. Which of the above definitions of information and order is most suitable for the study of biological development? Shannon's (3) is convenient, yet its reference to the observer's knowledge often evokes the objection that "information" is observer-dependent, hence not an objective physical quantity. Morowitz (1978), for example, clearly points out this subjective nature of information, although he does not regard it as a vice. We should prefer, however, Layzer's and Landsberg's formulations (10) and (11), because both potential and actual entropy can be objectively defined in probabilistic terms ("Actual entropy" has been written instead of Layzer's "observed entropy" to stress this point).

For the time being, this introduction will suffice. We shall try to clarify these concepts further as we go on.

4. The Minimal Assumption: Flexible Autocatalysis as the Crucial Condition for Life's Emergence

Addressing the problem of the origin of life, the sole assumption that is proposed is due mainly to Manfred Eigen: *Life began with the appearance of an autocatalytic (self-replicating) molecule.* Nearly four billion years ago, in "Darwin's pond", as biologists like to call the primordial lake or sea in which life supposedly emerged, a molecule was formed by chance, that had a peculiar capability: it initiated a chemical reaction that produced an identical molecule, thereby giving rise to a long-lasting process. This hypothesis will henceforth serve as the "Minimal Assumption" from which the emergence of life from inanimate matter should follow as a natural consequence.

Chemically speaking, this assumption refers to the process of catalysis, whereby a certain substance enhances a specific reaction. Could there be a catalytic molecule that leads to the synthesis of an *identical* molecule? What we are looking for is a reaction of the type:

$$R \xrightarrow{a} a + b \qquad (12)$$

where **R** stands for the reactants, a the reaction's product and **b** the by-products. The small letters denote microscopic quantitatives, while the capital letter denotes macroscopic quantities; italics denote single molecular species, while boldface denote sets of such species. As a plays the role of both catalyst and product, it is autocatalytic. Recent research has discovered few molecules capable of such activity (Emsley, 1990). For our purpose this is enough, for once the mere possibility of such a process has been demonstrated, one can study the universal thermodynamic laws that must govern it, regardless of its specific chemical details. So, for any autocatalytic molecule that could have ever been formed, the following rules must hold.

The number of the molecule's copies depends mainly on two quantities: its stability and its replication rate. Stability is restricted by the molecule's complexity. Von Neumann (1966) has shown that any self-reproducing automaton, in order to give rise to an exponentially growing number of copies, must possess a certain degree of complexity, below which the process would degenerate. This complexity, Von Neumann argued, is necessary in order to allow both the operation of the system and the sufficient information content needed for self-replication. In our case, the first requirement is not necessary: the molecules invoked by the Minimal Assumption do

not have to metabolize or to do any other work of maintenance, so even the little order that it possesses will not sustain for long: the autocatalytic molecule, whose production is a rare event, will sooner or later decompose, whether by means of a high-energy photon or by reacting with an active molecule, and, obeying the Second Law, its atoms will return to their more probable state:

$$a \rightarrow r. \qquad (13)$$

The molecule's stability thus assigns it some average lifetime, t_1. Its other crucial quantity is its average replication time, t_2. We are now in a position to make a simple mathematical statement. For any population of molecules, the decomposition rate is $1/t_1$. In other words, $1/t_1$ molecules decay during each time unit. Similarly, $1/t_2$ is the rate of replication. These two quantities determine together the population's size. The population's growth-rate, in accordance with Malthus' (1798) old observation, depends on the net-growth:

$$\frac{dX}{dt} = X\left(\frac{1}{t_2} - \frac{1}{t_1}\right), \qquad (14)$$

where X is the number of molecules. To find out the population's size at any moment, integrate (14):

$$X_t = X_0 \exp\left[\left(\frac{1}{t_2} - \frac{1}{t_1}\right)t\right], \qquad (15)$$

where X_0 is the population's initial size. (For the moment, we put aside environmental restrictions.) Let us begin with the appearance of the first molecule, $X_0 = 1$. For a slowly replicating molecule, where $t_2 > t_1$, it is likely that the molecule will decompose before creating any copy of itself. Even if it does not, sooner or later this will be the lot of one of its copies, terminating the process. If $t_2 = t_1$, a long-lasting closed causal loop may occur, yet it will remain at the mercy of chance, as each molecule might decay by accident before replicating. It is the third possibility that interests us, namely, $t_2 < t_1$. Indeed, most catalysts are capable of catalyzing many molecules before decomposing. Such a rate leads to an exponential proliferation of the autocatalytic molecules. Even if $t_1 - t_2$ is only slightly greater than zero, exponential proliferation will occur. *A crucial transition thereby takes place: a highly improbable, microscopic event, namely, the assembly of the autocatalytic molecule, gives rise to a deterministic process that, with increasing certainty, exerts macroscopic environmental effects* (Lifson, 1994).

Now, apart from the limit on the molecule's lifetime, the Second Law interferes with the process in yet another way. Replication involves information

transfer, information in this context being measured by the similarity of the new copy to the original one. Hence, the process is subject to the harassment of the Second Law (Smith & Morowitz, 1982; Weber et al., 1989; Eigen, 1992). Thermal fluctuations constantly inflict the molecular information with "noise" in the form of accidental errors occurring in the replication process.

What happens to an ill-replicated molecule? This is a crucial question. The error may affect the molecule's capability of replication, in which case it will leave the game. This might happen if the error affects the molecule's active site. If, on the other hand, it affects the molecule's inactive site, it will not cause any change in the next molecule. This leaves us with a process that can hardly lead to any real evolution. The molecules' form will remain the same through the generations. We must therefore add a constraint to our Minimal Assumption and demand that the primordial molecules be capable of "flexible autocatalysis", i.e. self-replication in which occasional changes in the molecule's structure are transmitted to its copies.

But is such a process possible? Here Eigen's (1992) model points out an elegant answer, supplied by Nature itself: *The DNA molecule is an enzyme whose active site creates the active site of another DNA molecule, in a very precise fashion*. Given a sufficient amount of nucleic acids in a solution, a strand of DNA can form another strand, in which each of the original four nucleic acids is replaced by its conjugate (Adenosine–Thymine, Guanine–Cytosin). True, this process is somewhat more complex than simple replication: the new DNA molecule is not identical to the original one but rather constitutes its complementary structure, but in turn, it creates another complementary molecule that is again identical to the first one. Some careful experiments by Orgel (1979) and Spiegelman (1967) have demonstrated the evolution of viral RNA strands in various *in vitro* conditions.

This example, although somewhat complex and at present known to occur only inside living organisms, shows that flexible autocatalysis is possible in principle. Any error in the DNA's replication process, where one nucleic acid is replaced by another, is transmitted to subsequent copies. Clearly, it must have been a much simpler molecule of this kind that was created by chance on the lifeless, ancient Earth, and simpler raw materials must have sufficiently abounded. This last requirement is fairly realistic in view of the present knowledge about the conditions on Earth prior to life's emergence: Miller's celebrated experiments (Miller & Orgel, 1974) have demonstrated the possibility of spontaneous assembly of

various organic compounds, including some amino acids like alenine, under experimental simulations of possible ancient atmospheres composed of methane, ammonia, molecular hydrogen and water, and with the presence of electric sparks. Other variants on Miller's experiments (see Shapiro, 1986) have also yielded encouraging results. De Duve (1991) has further substantiated Miller's conclusions by comparison with recent results from the analysis of meteorites, also found to contain many organic compounds.

To summarize, the Minimal Assumption is realistic and fairly likely. An autocatalytic molecule could, under reasonable conditions, have been formed long ago, flexibly self-replicating and thereby giving rise to a process which was long and stable and at the same time subject to constant changes. It is proposed here that this event was sufficient for the evolution of life to have followed as a natural consequence.

5. The Consequences: Feedback, Self-Resetting, and Entropy-Inversion

What is it in self-replication that endows matter with properties that are the pre-requisites for life? Notice first that this is a cyclic process: each event is the cause of an identical event that, in turn, constitutes the cause for the next identical event. This grants the process a certain degree of *autonomy*, as it perpetuates itself as long as energy is available. In fact, this is a *feedback* mechanism, and if autocatalysis is flexible, as we assume, this feedback can be of either sign: a stable molecule produces many other copies that will again proliferate on their turn, and conversely for an unstable molecule. These two phenomena, feedback and autonomy, are the main characteristics of life.

But the cyclic nature of autocatalysis grants the process an even more crucial capability, easy to comprehend once we recall engine operation. Any machine, in order to be capable of *continuously* converting energy into specific work, must be capable of constant *resetting*, i.e. returning to the initial state. This way, for example, a turbine can utilize the energy of water, wind, etc, while other objects can be driven by the same energy to perform only a little work before undergoing an irreversible change. Resetting is similarly vital for all information-processing systems: The film in the camera, the white paper in the typing machine, etc, "reset" after each irreversible operation so as to enable the system to be ready for the next one.

The role played by self-replication in living systems is similar. Life, as we shall see below, is a process capable of both doing work and incorporating

information continuously, without being irreversibly worn out in the process like all other objects affected by natural forces.

But merely resisting irreversible wearing out is not enough. Can a natural process further cheat the Second Law so as to *invert* its operation? Self-replication reaches this goal by another of its inherent peculiarities, namely, the exponential proliferation it manifests whenever $t_2 < t_1$. As noted long ago by Malthus (1798), an exponential growth rate inevitably leads to clashes with environmental limitations. As soon as the available energy and chemical raw materials are overconsumed, autocatalysis has to slow down and stabilize. The population's size is therefore restricted by the Lotka–Voltera equation (in Schneider, 1988), which, adapted to our notation, reads

$$\frac{dX}{dt} = X\left(\frac{1}{t_2} - \frac{1}{t_1}\right)\left(\frac{K-X}{K}\right), \qquad (16)$$

where K is the upper limit of the population and $(1/t_2 - 1/t_1)$ the unrestricted rate of the population's growth. Notice that the term $K - X/K$ denotes the role of negative feedback. As the population grows, the rate of its growth decreases and vice versa.

This negative feedback creates a unique mechanism of entropy inversion. Following Von Neumann's (1966) above reasoning, we regard every autocatalytic system (whether a molecule or a living organism) as an ordered system. The competition between the ordered systems leads to a peculiar result:

(i) *Every replicating system is both an order-maintaining and an order-inhibiting system.* As long as it exists, preserving its own order, it hinders the creation of other ordered systems. In the case of animals and plants, this is due to depletion of air, food, etc. In the case of autocatalytic molecules, this is due to depletion of reactants. This double role of the autocatalytic system leads to a complementary peculiarity:

(ii) *The destruction of any autocatalytic system enhances the creation of another.* If the system is an autocatalytic molecule, it releases reactants as it decomposes, increasing the likelihood for the formation of another molecule. If it is a living organism, the effects are more diverse. Any rabbit that has fallen prey to a wolf increases the survival and reproduction

chances of fellow rabbits by satisfying the predator's hunger for a few hours, by leaving scarce plants ungrazed and females free to mate with. The population's attraction to the equilibrium point K thus creates a thermodynamic action–reaction process: for any part of this ordered population that succumbs to disorder, another part automatically expands to the same degree. This spontaneous entropy inversion gives rise to the third and most crucial evolutionary characteristic:

(iii) *If the destruction is systematic, i.e. it eliminates only systems with certain traits, then the reaction of the population is also systematic: it increases the number of systems with the opposite traits.* And indeed, the destruction *is* systematic: natural selection is exerted by fairly constant environmental conditions that prevail for long periods over large areas. Such a systematic action, then, invokes an equally systematic reaction: the population prospering in the void left by the part that has perished has traits that faithfully correspond to those of the environment.

It has thus been proved that a population of autocatalytic molecules is capable of incorporating information about the environment, enabling adaptation to that environment. The details of this evolutionary incorporation of information is studied in the next section.

6. The Proto-Cognitive Model: Evolution as an Information-Gaining Process

In what follows it will be shown how the molecules invoked by the Minimal Assumption could have undergone evolution in the full sense of the word. Moreover, this evolution exhibits many primordial capabilities of cognition. Many authors (see Elitzur, 1994b) have pointed out striking similarities between evolution and the main characteristics of intelligence, such as cognition, learning and even scientific research. An article by Heschl (1990) claimed that life and cognition should be straightforwardly equated, and a similar argument has been made by Marijuán (1991). Grossman (1992) has shown how the immune system is capable of learning, remembering and discriminating different signals by their strength. Cohen (1992a,b) has extended the notions "cognition", "language", and even "meaning" to the operation of the immune system. The Proto-Cognitive Model proposed here puts forward a broad generalization of these arguments, founded, step-by-step, on the simplest considerations.†

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† Proto-cognitive is a generalization of the term "ratiomorphic", coined by Brunswik (quoted in Lorenz, 1973) to denote seemingly intelligent instinctive behaviors of low organisms. As instinct is an example of a highly intelligent action occurring in the absence of intelligence, the same observation holds for evolution as a whole.

My aspiration is therefore two-fold: while the following discussion deals with the presumed prebiotic evolution, the arguments equally hold for evolution in its present form. Hence, for every occurrence of the word "molecule" one can read "animal" or "plant" instead. In all cases, evolution will be shown to be a primordial form of cognition.

6.1. SIGNAL RECOGNITION AND RECORDING

We begin with a highly simplified case. Consider the information carried by a population in which a certain mutation has appeared by chance. Let the probability for a mutation to occur in one molecule be q, so the probability for its occurrence in n molecules by chance (i.e. independently) will be the product of the separate probabilities, namely, q^n. Conversely, the chance for the occurrence of such a mutation in n molecules out of a larger population, namely, X, is proportionately larger:

$$P = C_x^n q^n (1 - q)^{x-n}, \tag{17}$$

where C_x^n is the binomial coefficient.

For simplicity, we take a population of 100 molecules, where $100 = K$, the upper limit on the population's size given in (16). Also, let the number of possible mutations be 9, so that together with the original molecule there are 10 possible forms. Keeping the convenience of decimal figures, let the probability for each mutation be $\frac{1}{10}$. To make the process realistic we assume that this mutation is reversible, i.e. there is the same probability for a mutated molecule to mutate again. Figure 2 represents the population under study. Black circles represent molecules affected by one particular mutation, while the white ones represent the other nine.
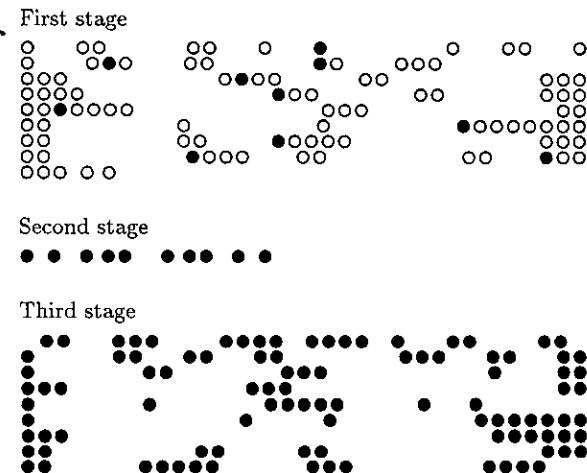

FIG. 2. The information carried by a population of self-replicating systems.

We leave the population to itself, with no environmental interference save the above limit $K = 100$ and the inherent limit on the molecule's average lifetime, t_1. Eventually, the population will evolve towards the state with the greatest likelihood, i.e. equilibrium, where all mutations number the same. About 10 molecules would possess the particular mutation (black circles). Here we notice an important relation between a macrostate and its microstates: The probability for any 10 molecules out of 100, P, is the sum of many probabilities p_i of various arrangements of individual molecules. There are, of course, many such possible arrangements, which means that the entropy of this state is high. Indeed, considering q, this state has the highest probability,

$$P_1 = 0.132, \tag{18}$$

and consequently the highest entropy as well. Applying (2), we get the state's entropy by calculating all the p_is

$$S_1 = -k \sum_{i=1}^{w} p_i \ln p_i$$

$$= -k \sum_{n=0}^{100} C_{100}^n p_n \ln p_n$$

$$= -k \sum_{n=0}^{100} P_n \ln p_n.$$

For $n = 10$,

$$= -k P_{10} \ln p_{10}$$

$$= -k\, 0.32 \ln[(\tfrac{1}{10})^{10}(\tfrac{9}{10})^{90}]$$

$$= -k\, 0.32(90 \cdot \ln 9 - 100 \cdot \ln 10).$$

Taking $k = 1$ for convenience,

$$= (-1) \cdot (-4.287) = 4.287. \tag{19}$$

How much information is carried by such a population? Here, the observed entropy equals the maximum entropy, so, applying (10),

$$I_1 = 0. \tag{20}$$

Now suppose that the environment has undergone a change that is destructive for all the molecules save those possessing the mutation. The population would soon shrink to $X_2 = n$, but now all of its members would possess the mutation. The probability for such a state to occur by chance drops back to

$$P_2 = q^n, \tag{21}$$

and in our case,

$$P_2 = 10^{-10}. \tag{22}$$

The entropy here is

$$S_2 = 2\cdot3 \times 10^{-9} \approx 0. \tag{23}$$

In order to define the information carried by this population, we define its maximal entropy. The most probable state of this ten-molecule population is about one mutation, $P = 0\cdot387$, and the maximal entropy is accordingly $1\cdot26$. Applying (10) again, the information will equal the maximal entropy:

$$I_2 = 1\cdot26 - 0 = 1\cdot26. \tag{24}$$

Now, since $X = K$ is the upper limit on the population enforced by the environment, as in (16), the remaining population will soon proliferate back to the size of the original population, but now all molecules possess the mutation. The probability for this state to occur by chance is extremely small,

$$P_3 = 10^{-100}, \tag{25}$$

yielding the entropy

$$S_3 = 0, \tag{26}$$

which, subtracted again from the maximal entropy, given in (19) above, gives the information of the new population. This time we have an enormous amount of information about the new state of the environment:

$$I_3 = 4\cdot287. \tag{27}$$

Formulated non-quantitatively, the population has reacted to the environmental change with a stable counter-change. One who observes this counter-change in the population can infer with great certainty that a change has taken place in the environment.

The analogy between this form of evolutionary "learning" and cognitive processes is striking. In evolution, the destruction of one mutation leads to an equal proliferation of its competitor. In rational inference, the negation of one possibility lends additional likelihood to the remaining one(s). Evolution employs the same logical operation, to which it has added just one crucial ingredient: mutations keep enlarging the number of possibilities, thus making evolution a truly creative process.

6.2. SIGNAL MEASUREMENT AND RESOLUTION

Of course, evolution does not work in such a simple all-or-none manner. Yet, if such an unrealistically simple model is capable of information extraction and recording by a population, we can expect the process to be much more interesting once we make it more realistic. At this point, it is necessary to introduce a very powerful principle of evolution, the

importance of which cannot be overemphasized. I call it "the all-or-none-or-anything principle": *Evolution does not merely distinguish between fitness-survival and unfitness-extinction; it reacts in a very precise, quantitative manner to the entire spectrum of intermediate cases.* After all, no organism really survives. It is only that some die later than others. Once this mathematical aspect of evolution is taken into account, it will reveal evolution's full ability of extracting information about the world.

Consider the primordial molecules' stability, which determines the time span of their existence. From (15) it is clear that a molecule's stability quantitatively determines the number of copies that it produces before decomposing. Such a fairly accurate conversion of one quantity into another, i.e. longevity, into a number of copies, makes the process analogous to *measurement*. Moreover, it is a very delicate measurement in that a microscopic quantity, namely, a molecule's stability, is amplified by the number of replicated molecules into a macroscopic quantity.

Now consider a slight change taking place in the environmental conditions, that gives only a slight advantage or disadvantage to a certain mutation. This change, however small, leads to an important statistical effect. While it gives only a little guarantee for the survival of an individual molecule, the difference becomes noticeable on large populations. A single molecule might by chance encounter too harsh or too hospitable conditions under which its advantage is not put to test at all. Its survival is therefore random, only loosely related to its structure. However, autocatalysis gives rise to the operation of a powerful statistical law: *Large numbers turn a probabilistic effect into a deterministic one.* Replication thus liberates the mutation from the whims of chance, and even a small advantage exerts a noticeable effect when the population is large.

This differential magnification is analogous to some common resolution techniques used in scientific research, such as centrifugation and chromatography. When two chemicals with densities a and b differ only slightly in their densities, the above techniques increase their effective densities by a certain multiplier, thereby increasing by the same multiplier the *difference* between them: While

$$\frac{Ka}{Kb} = \frac{a}{b}, \tag{28}$$

nevertheless, for $K > 1$,

$$|Ka - Kb| > |a - b|, \tag{29}$$

and K can be made large enough to magnify even small differences. A much greater resolution is yielded

by the amplification through replication. Applying (15) to an arbitrarily small difference between the average lifetimes of two molecules, $t_{1'}$ and $t_{1''}$, where $t_{1'} > t_{1''}$, and assuming equal initial populations and equal rates of replication, we obtain for their populations X'_t and X''_t the ratio

$$\frac{X'_t}{X''_t} = \frac{\exp\left[\left(\frac{1}{t_2} - \frac{1}{t_{1'}}\right)^t\right]}{\exp\left[\left(\frac{1}{t_2} - \frac{1}{t_{1'}}\right)^t\right]} = \exp\left[\left(\frac{1}{t_{1''}} - \frac{1}{t_{1'}}\right)^t\right]. \quad (30)$$

This converts even a slight advantage into an exponentially increasing difference between the two populations. Thus, even a weak environmental factor gives rise to a change that would eventually dominate the whole population.

This amplification of relative differences, which would have been notable even in an unlimited environment, is enormously increased by a factor encountered earlier, namely, the competition between the molecules over finite resources. It has been noted that the very decay of an unfit molecule increases the probability of other molecules to survive, and conversely, successful mutations decrease the survival chances of other ones. The equilibrium between the mutations, even if it has been initially stable, is thereby increasingly upset until a more stable equilibrium is reached (Robertson, 1991). These irreversible processes grant the population an effective mechanism of *memory*, enabling beneficial changes to be stably "recorded" on the entire population.

6.3. AMPLIFICATION OF SIGNAL-TO-NOISE RATIO

The exponential growth grants the self-replicating population yet another important mechanism of information processing, namely, elimination of noise. The analogy with the Newtonian telescope is instructive here. The information coming from a star is quite poor. The reason for this information degradation is not, as one might think, only the depletion of the light's energy, for otherwise the information could be increased by mere electric amplification. Rather, it is the random fluctuations (atmospheric and optic) that distort the diminishing light. Consequently, since the human pupil with its few millimeters diameter receives only a small quantity of light, this light is severely affected by such noise. The Newtonian telescope tackles this difficulty by a concave mirror with a large diameter, sometimes up to a few meters, that

collects the light signals over a large area and concentrates them on the telescope's lens. The same operation is performed by all antennae. Here an interesting resolution of signal from noise takes place: *The constant signals are additive, while the fluctuations, being random, are much less so. Hence, the sum of many measurements yields a much better signal-to-noise ratio.*[†] Let s and Δs denote signal and noise, respectively. Then, after n measurements,

$$\frac{s}{\Delta s} \rightarrow \frac{ns}{\sqrt{n}\Delta s} = \frac{\sqrt{n}s}{\Delta s}. \quad (31)$$

In evolution, whether biotic or prebiotic, replication ensures a very large n, so any signal inherent to the macroscopic environment, however weak, is retrieved in the long run, despite microscopic fluctuations.

6.4. RECOGNITION OF ABSTRACT INVARIANCES

The distinction between signals and noise needs further elaboration. A rock contains some information about its environment in the form of numerous marks left on it, yet these marks concern only immediate events in space and time. In contrast, the information embedded in a potato of the same size concerns features of the environment that are much more prevalent in space and time.

At higher levels of evolution, the environmental features detected by the organism are so subtle that they often give the impression of having been discovered by highly sophisticated scientific means. Organisms are capable of detecting not only residual chemicals or weak fields, such as the pole's upward magnetic field detected by some bacteria (Gould, 1980), but also abstract features like periodicity. Such as the case, for example, with those cicadas whose life cycle takes 13 or 17 years (Gould, 1977b). What is amazing about these lifecycles is that there are *three distinct species of cicadas*, each of which is divided into two subspecies, one with 13- and the other with 17-year life cycles (Dawkins, 1987). According to the prevalent explanation, it is not a coincidence that these periods are prime numbers: they prevent convergence with the life cycle of a predator (unless it happens also to be 13 or 17). More impressive examples, often pointed out in the sociobiological literature, give the impression that the organism masters the advanced mathematical knowledge needed for its sophisticated reproduction strategies (Dawkins, 1989). Again, replication provides an efficient means for the detection of such abstract features of reality. As we noted above, (31), the statistical effect of the overall sum of organism–environment interactions guarantees that the noise of irrelevant effects would gradually diminish,

[†] Although no one has yet pointed out this thermodynamic aspect of the telescope, one only has to recall the patient and laborious work needed for the appropriate polishing of the mirror. This is the price paid for the local reversal of the light's entropy.

leaving only the essential signals to produce significant marks.

Notice, however, that "signal" and "noise" are somewhat relative terms. A certain environmental feature that resides over a large area constitutes a signal, yet when many different environments are scanned together these local signals turn into noise. The new signal that has to be extracted beneath this noise is a more subtle, fundamental environmental feature. Evolution can thus be characterized as pursuing more and more subtle signals, leading to a growing *abstraction* of the information it incorporates. Consider a mold colony: its shape gives a very precise mapping of the area in which the nutrients abound. The nature of the information possessed by each individual mold concerns only its tiny local surrounding, and the geographical information exhibited by the entire colony can be used only by a more intelligent observer who looks at it. Ascending on the botanic tree, the next organism to be considered is the creeping plant, which assumes the shape of the neighboring objects. This information is broader than that of the mold, and is used by the plant as a whole and not only by its separate cells. Also, by phototaxis the plant reacts to distant light sources. Still, the plant's shape mainly reflects the close surroundings. The next level, that of a tree, represents perception of more subtle factors: the mechanism of negative geotaxis responsible for the tree's upright posture relies heavily on the gravitational field, but still every tree has an individual shape reflecting the local conditions in which the tree is placed all its life. The next level is represented by trees like the fir or the cypress, that have a constant shape. Interestingly, these trees' shape is not only constant but also radially symmetric, the tip pointing precisely upwards. Here, the reliance on the global gravitational field leads to a considerable autonomy in relation to local conditions, as can be seen in trees growing on a slope.

These few comments hardly do justice to the fascinating issue of biological morphology: a discussion of purely biological evolution is not possible here. But one more general observation is in order. When we survey the living kingdom we see that, unlike most plants, the organisms belonging to this kingdom have a constant form. The reason is simple: they are in constant motion, so they cannot adapt their form to local conditions. This regularity in form gives rise to an even more striking regularity: all animals are symmetric in the direction perpendicular to that of their preferred posture and to that of their motion.

† To illustrate this principle recall the form of man-made vehicles: they too are symmetric in the direction perpendicular to that of their preferred posture and to that of their motion.

The reason for these two biological constants is clear: the animal's regular form reflects adaptation to those environmental conditions that are equally likely to prevail in all the sites in which it passes, and symmetry reflects adaptation to interactions that are equally likely to occur to it on both sides.†

To summarize, organismic information develops towards generality, so as to enable independence of local variations. To use the parlance of theoretical physics, the evolving system gradually recognizes natural *laws*. These laws, like basic physical laws, become increasingly invariant. The laws embedded in the long-lasting organism are "invariant under time translation". The laws embedded in the mobile organism's shape are "invariant under space translation". And the laws underlying the organism's symmetry are "invariant under space rotation". Is it only a coincidence that symmetry is both the touchstone of sound physical laws and an inherent feature of so many biological structures?

6.5. CONTROLLED EXPERIMENTATION WITH MANY VARIABLES

Evolution has been likened here to cognition owing to its ability to extract information from the environment. In fact, we can liken it to an even more advanced mode of gaining knowledge about reality, namely, to scientific research. The above analogies to some scientific instruments are not coincidental. Evolution performs something even more delicate than measuring and recording environmental conditions. A process in which several identical molecules are subjected to similar conditions is analogous to a reliable *experiment*. Each copy of the molecule constitutes an independent replication of an experiment in survival—more particularly, the survival capability of that particular structure. The large number of experimental replications gives high credibility to the overall result.

Once we take mutations into account, the analogy to a scientific experiment would become even more appropriate: We have an "independent variable", namely, the molecular structure that slightly varies between individual molecules, and a "dependent variable", which is the number of copies that every molecule eventually produces. The graph in Fig. 3 depicts a simple example of such a causal dependence: The S axis represents a structural parameter (say, size). Each value of S gives rise to a corresponding value of X, namely, the number of replicated copies. As replication goes on the mutations will eventually occupy a wide range on the S axis, giving rise to the entire spectrum of the corresponding X values. Since the function that relates S with X is often non-linear,
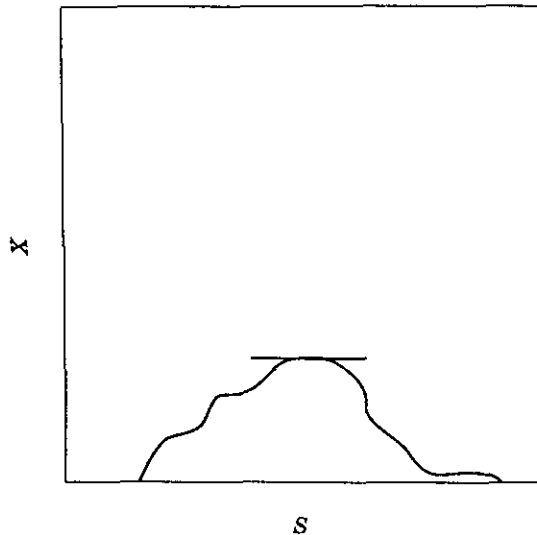
Fig. 3. A schematic relation between a structural variable of a self-replicating system and the number of its offsprings.

it is very beneficial to measure the rate by which X changes with S. Mathematically, this means taking X's derivative. Indeed, this is what the evolutionary process does. When the replication rate is high enough, then, for two molecules or organisms that differ only slightly in some physical parameter, the differences in the number of their offsprings would become noticeable (30). The process is thus capable of yielding $X_2 - X_1/S_2 - S_1$ where $(S_2 - S_1) \rightarrow 0$, which is dX/dS. Moreover, notice that in this case the graph forms a crude Gaussian curve, $S = m$ being the maximum point beyond which the structural variable (e.g. size) turns from an advantage to a disadvantage. Around such points at which S yields the highest X, there are consequently many copies and, therefore, many mutations. In this area, then, the measurement will be more and more refined, new mutations continuously feeling that area of S, until a highly accurate value of the point where $dX/dS = 0$ is obtained, i.e. the precise S that yields the maximal X.

The above case is, of course, of a simplified one, where the relation between S and X can be expressed by an ordinary differential equation. But the same holds even for completely chaotic relations between the two variables. The very "primitive" nature of the evolutionary method, namely, blind trials unsystematically carried out on numerous Ss, allows it to find even the most bizarre singular points.

Any reliable experiment must include "experimental" and "control" groups, in order to assure the experimenter that only one variable, the one omitted in the control group, is responsible for the experimental result. Our prebiotic experiment includes this setup in its very design. Mutations give rise to experimental

and control populations, and the comparison between them is made by their very competition. The environment also supplies its variables to the experiment. As molecules replicate, they spread in the medium in which they reside, encountering conditions that significantly differ from one site to another. This introduces a new set of variables into the experiment. If autocatalysis is intense, it will eventually test all the structural variables against all the geographical ones, eventually giving rise to the best matches.

Evolution therefore constitutes a huge, multivariable experiment that studies simultaneously, through a myriad of parallel interactions, the fitness of a certain structure plus/minus one physical unit to a certain environment plus/minus one local condition. Each molecule–environment interaction provides a control experiment for a certain variable which is present in another interaction. Thus, the specific contribution of each variable to the survival test is eventually *isolated*, i.e. tested separately.

Proceeding for a moment from prebiotic to biological evolution, we notice that the development of sexual reproduction constitutes a considerable refinement of this proto-cognitive ability. It is common to think of the aim of sexual reproduction in terms of information sharing, but, from the viewpoint of information theory, it has a more fundamental function, namely, signal resolution. Before sexual reproduction evolved, an organism survived thanks to the total *sum* of its genes, advantageous as well as disadvantageous. It was a crude experiment which did not make it possible to know which of the variables was responsible for the success. Consequently, in the next generation, that organism's offsprings possessed all their parent's qualities. The "experimenter", as it were, had no choice but to repeat all the variables of the previous experiment. Only during several later generations, after random mutations have eliminated one gene or another, has the advantageous trait been tested alone. This pre-sexual stage parallels pre-critical forms of knowledge. Often, when a child or a superstitious person wants a desirable event to recur, he or she repeats everything he or she happened to do prior to that event, failing to distinguish between relevant causes and irrelevant coincidences. Such a distinction comes only later with the maturation of thought. Similarly, primitive evolution has undergone a primordial phase of "crude learning" before sexual reproduction made it possible to isolate different mutations and subject them to separate probing.

6.6. INDUCTION

Detection and accumulation of separate units of information does not exhaust evolution's

proto-cognitive capabilities. Evolution is capable even of deducing new "conclusions" from these elementary units. For example, many animals possess eyes, the chemicals in which are excited by solar radiation, as well as metabolic reactions triggered by this radiation. These mechanisms indicate that the animal possesses inborn information about the sun's light as well as information about the sun's heat. On the basis of these separate units of information, several animals are capable of using the elongation of daylight as a sign for the coming arrival of the summer, and they begin to adapt their metabolism to it long before the increase of temperature. In other words, evolution has made a successful *induction*, detecting a correlation between the two phenomena and making the correct inference.

6.7. REFLEXIVE SELF-INSPECTION

The competition between autocatalytic molecules or organisms adds an important dimension to evolution's proto-cognitive nature. A system that has to compete with other systems must acquire information not only about the environment but also about other information systems. This parallels the *reflexive* stage in the development of intelligence, where knowledge progresses by the knower's self-examination. This reflexive trait is typical to evolution as a whole: *As evolutionary feedback loops become longer, not only organisms, but evolutionary processes as well, are subject to Darwinian principles.* Suppose, for example, that a certain species develops a higher reproduction rate. As we have seen earlier, this is an advantage not only for the survival of the organism but, in the long run, it guarantees that whatever other advantages that will appear in this species, will be more notice-able. This is an advantage of a higher order, namely, advantage in the very development of advantages. This way, evolution puts to test its own strategies as well (Gatlin, 1972 refers to something similar when discussing "second-theorem evolution"). The cicadas mentioned above, who can boast impressive mathematical achievements, manifest similar second-order knowledge: their discovery of primary numbers is based on many other discoveries made earlier by their predators, who arrived at the optimal number of years suitable for their life cycles. Evolution owes much of its intriguing ingenuity to this self-critical ability, mistakenly regarded as unique to *Homo sapiens* alone.

6.8. SUMMARY

Self-replication, whereby the system's lifetime is fairly reliably converted into the number of its offsprings, grants evolution a strong tool for extracting information from the environment. Evolution, as it were, performs reliable measurements and experiments, records and processes environmental information. The parallels, in fact, extend even to highly advanced scientific modes of studying reality.

A word of caution now has to be added. A model of prebiotic evolution, however detailed, still does not tell how such an evolution could eventually give rise to evolution in its present form. How could autocatalytic molecules evolve into organisms, capable of elaborate metabolism and possessing enormously complex bodies? A detailed discussion of this issue is not possible within the present framework. Elsewhere, Elitzur (1994*b*) has pointed out the direction where the answer should be looked for. Very early in the course of prebiotic evolution, it entered an *ecological* stage, where the selection pressure on the molecules was exerted not only by the environment but also by the molecules themselves on one another. The increasingly complex inter-molecular relations that ensued made possible the appearance of sexual reproduction, metabolism and a variety of complex structures. A "generalized biogenetic law", proposed in that study, shows how processes that took part in the evolution of populations were later internalized by the individual organism.

7. Maxwell's Demon and its Living Relatives

The heavy reliance on the concept of information in the above discussions may lead one to ask whether the assignment of such a central role to information in biology is not an exaggeration. In this section this question will be addressed in detail. The study of life in terms of information can provide the only satisfactory explanation for the enormous amounts of order generated by living systems. A simple exercise will make us realize the acuity of the problem posed by biological order.

An attempt will be made to assess the cost of an imaginary scientific project aimed at the artificial production of a single bacterium in all its microscopic details. The thermodynamic imperative, according to which the assembly of a structure must take energy proportionately to the structure's order, becomes much stronger when the structure is of microscopic magnitude: the smaller the volume of matter, the more violent are its fluctuations. For example, in a volume of a sphere with the diameter of one micron—about the size of an organnelle—there are on the average only 12·6 hydrogen ions, making pH fluctuations very hard to control (Johnson, 1987). In view of such difficulties it will be no exaggeration to estimate that such an "artificial bacterium" project

would demand several times more labor and energy than the project to send man to the moon. And yet, a single bacterium performs this task in 20 minutes, with negligible energy and from the simplest raw materials. Extending these considerations to multi-cellular organisms would make the riddle even more intriguing.†

Such biological feats are highlighted by the intriguing paradox known as "Maxwell's demon" (Ehrenberg, 1967; Tribus & McIrvine, 1971; Bennett, 1987; Leff & Rex, 1990a, b, c), realized long ago to be closely related to the riddles of life. Equally profound is the paradox's resolution, yet only a few authors have so far appropriately applied this resolution to the case of evolution, one reason being that the debate is still alive among physicists (see, e.g. Landauer, 1989; Leff & Rex, 1990b). In fact, as the resource bibliography of Leff & Rex (1990a) indicates, only a few authors have discussed the "demon" in the biological context.

The paradox is this. Maxwell proposed a thought experiment involving a tiny demon, residing inside an adiabatically closed container full of gas in a state of maximal equilibrium. This demon, Maxwell argued, might be able to decrease entropy by opening and closing a slit in a partition dividing the vessel (Fig. 4). This way, effortlessly concentrating fast molecules in one half of the vessel, the demon can increase order by concentrating heat in that half without dispersing significant amounts of energy. Even more simply, he can reverse by the same method the entropy-increase illustrated in Fig. 1. These are, of course, violations of the Second Law.

Following the paradox's publication, some scientists argued that such demons indeed exist—being the living organisms—and that the alleged violation of the Second Law proves that life transcends physical laws. Lord Kelvin, one of the formulators of the Second Law, accordingly chose the following formulation: "It is impossible, by means of an inanimate material agency, to derive mechanical effect from any portion of matter by cooling it below the temperature of the coldest of the surrounding objects" (Ehrenberg, 1967; Leff & Rex, 1990b). By this restriction to inanimate phenomena, Kelvin simply exempted life from the thermodynamic prohibition. Von Smoluchowsky, who elaborated other variations of the paradox, pointed out in 1913 another necessary qual-
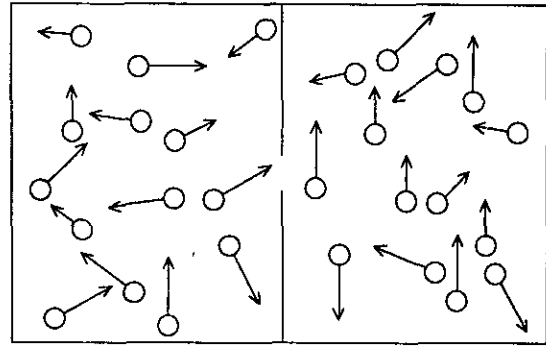
† In fact, I have made the demand from the imaginary scientific project too easy by allowing its workers to study the structure of a living bacterium before creating an artificial one. A stricter test of the cost of this project should demand the production of a creature that functions like a bacterium in all observable respects, without inspecting the bacterium's internal structure.

Fig. 4. Maxwell's demon can sort slow and fast molecules (circles with short and long arrows, respectively) by selectively opening the slit.

ity of the demon as the one enabling him to reverse entropy, namely, intelligence (Ehrenberg, 1967). In other words, he granted mind, rather than life, the ability to transcend physical law.

Maxwell's demon was exorcised only at the midst of this century by Szilard and later by Brillouin (1956, 1964). Szilard replaced Smoluchowsky's notion "intelligence" with "information" as the condition for the demon's succeeding in his prank. Brillouin has shown more particularly what the demon must do: he needs to know the momenta of the molecules approaching the slit in order to open or close it at the right moment. Since the gas in the vessel is in complete equilibrium, making vision impossible, the demon must use additional light in order to acquire the information he needs. This would increase the overall entropy of the system more than the entropy decreased by his sorting. It thus became clear that information acquisition, transmission and processing require proportionate exchanges of energy in parallel.

Recently, Bennett (1987) and Landauer (1989, and references therein) arrived at a more precise solution: the thermodynamic cost of the demon's acquisition of information does not always lie in the act of measurement, since under certain conditions measurement can be a reversible operation that does not increase entropy. What always must increase entropy is the erasure of previous information before a new measurement is carried out. This argument deals with an idealized case. When applied to practical cases, it implies that at each step the demon must increase the entropy twice, once in measuring the molecule's position and again in resetting his memory (Bennett, 1987). Dealing with the case in which the demon (in the form of an automatic engine) has a big enough memory so that he does not need to erase the results of previous measurements, Bennett states:

The correct thermodynamic interpretation of this situation would be to say the engine increases the entropy

of its memory in order to decrease the entropy of the environment. (p. 96)

The relevance of this discussion to biology is now evident. The resolution of Maxwell's paradox renders memory a crucial ability required from the demon. Significantly, *this is exactly what our Minimal Assumption points out as the most crucial characteristic of biogenesis and evolution*. Molecular replication consists a primitive yet very accurate memory. Another crucial feature of evolution pointed out in Section 5, namely, constant resetting, takes its thermodynamic cost too. The resolution of Maxwell's paradox thus provides a sound explanation for such striking feats of biological order-generation as demonstrated by the bacterium considered above. A few more examples will illustrate in more detail how living organisms constitute law-abiding demons.

A gull travels far west while alternating winds are blowing in all directions. This is done by selectively exploiting the winds that blow towards the bird's destination, while resting when other winds blow (one is often struck by the graceful lack of effort in these birds' flight). Similarly, a lizard in the desert, threatened by excessive heat during the day and equally hostile cold at night, manages to maintain a tolerable temperature most of the day just by changing its position during the hours. The similarity to the demon's operation is clear. In both examples, we now notice, the "demons" succeed to maintain and increase their order by knowing in advance (i.e. by inborn instincts) the environment's essential dynamics. In fact, living organisms are Maxwell demons in a more fundamental sense. The organism begins its life on the molecular level where, like the demon, it directs molecular interactions with the aid of the appropriate enzymes to create the enormous macroscopic order of a large body. While this may not look surprising in the case of the whale, whose fertilized egg develops within the highly nourishing womb, this is certainly impressive in the case of the oak seed that builds a huge tree out of soil, water and air alone. It is the genetic information that enables the generation of such huge amounts of order with so little free energy.

Morowitz (1978) has presented Maxwell's paradox in a form that is of special interest for the biologist. He pointed out that the demon can turn heat, the least efficient form of energy, into mechanical energy. In other words, bound energy is converted into free energy, against the direction dictated by the Second Law. Monod (1971) and other authors quoted by Marijuán (1991) argued that enzymes are Maxwell demons. Indeed, enzymes' ability to turn thermal into chemical energy is a Maxwellian task. In this case too, the correspondence between the shape of the enzyme

to that of the substrate provides the information necessary for accomplishing this task.

Consider the analogy between the imaginary demon and the living organism in greater detail. What is the "container" in the real situation? If the container is the environment as a whole, than the biological demon faces a much harder task than the theoretical one. While Maxwell's demon is inserted into the initial conditions of the experiment as a fully-fledged demon possessing its own reservoir of energy and intelligence, this is not so with the living creature, who must take its own energy from the systems it operates on. Conversely, if the "container" is the organism's body, then the demon must first build the very container within which it would create the border. This is harder than the demon's task.

Yet, in another respect the organism's task is easier since in the demon's case, the complete equilibrium inside the container rules out any extraction of information from the environment. Our actual world, in contrast, is far from equilibrium (Tribus & McIrvine, 1971). It is full of energy sources, spatial and temporal regularities, and complex compounds. The organism is therefore bombarded with information, thanks to which it succeeds in a Maxwellian task: with little energy it creates highly complicated systems, the assembly of which out of complete disorder would require immeasurable amounts of energy. Hence, if we want to make Maxwell's demon analogous to living organisms, we must picture the molecules' motion in the vessel as a more ordered process, say, molecular "flows". Under such conditions (Fig. 5), the demon needs not carry out preliminary measurement. Rather, any random opening or closing of the shutter constitutes in itself a primitive form of measurement: If, after opening the shutter, a fast or slow molecule has passed from one part to another, then the demon can leave the shutter open or closed, as the case may be, because this molecule probably foretells a group of other molecules with the same momenta.
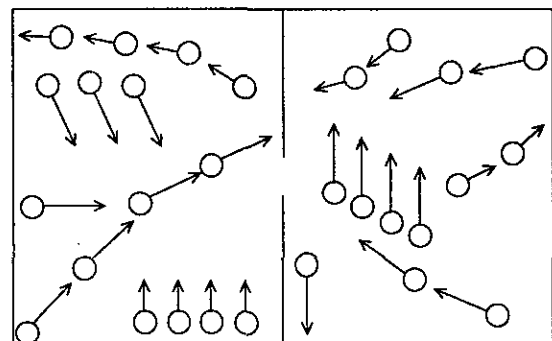

Fig. 5. An ordered gas allows the demon to perform the sorting.

The analogy is now clear: evolution resembles our modified experiment in that every mutation is equivalent to a random decision of the demon to open or to shut the slit, an action which serves as a measurement. Owing to environmental order, each such a measurement provides some information about future states as well. An organism that survived constitutes a measurement that have revealed a regular pattern in the environment. The resulting gain in order is used for the assembly of the demon's offsprings, who would repeat their ancestor's measurement that have already detected a stream of environmental order.

All this substantiates Schrödinger's controversial insight that the living organism maintains its order by "continually sucking orderliness from its environment" (Schrödinger, 1945, p. 75; see Elitzur, 1994b). Later authors have coined the abbreviation "negentropy" for this negative entropy. Schrödinger has made a very surprising observation to prove his argument: the organism does not eat in order to get energy from the food; it could as well just conserve the energy of much less meals for its entire lifetime. Rather, it eats for the *order* in the food. Plants, the most basic form of food, take this negative entropy from the Sun, the source of high-energy photons. Overall, the biosphere radiates back the same amount of energy as it absorbs, but the radiated energy has higher entropy (Penrose, 1989). This was pointed out long ago by Szent-György (1957), who referred to the Sun as the source of all our negative entropy. Morowitz (1978) has emphasized that "it is not energy *per se* that makes life go, but the flow of energy through the system" (p. 161). In other words, there should be an energy gradient, in an environment far from equilibrium, for life to be able to use this energy.

Let us put the negative-entropy concept in more recent terms. The entropy-growth of a dissipative system is expressed by Prigogine's (1955) equation

$$dS = dS_i + dS_e,\qquad(32)$$

where dS_i stands for the system's internal entropy production and dS_e denotes the entropy exchanges with the environment. dS_i must always increase unless the system is in complete equilibrium, that is, dead. The only way for the system's growth of order is, therefore, through dS_e, namely,

$$dS_e < -dS_i < 0,\qquad(33)$$

which can happen under one of two conditions: either the entropy exchange with the environment goes from the system outside, or the entropy coming from the outside is negative.

The former possibility takes place when the organism dispenses with waste-materials. The latter possibility, however, is what Schrödinger had in mind. The resolution of Maxwell's demon is thus fully consistent with his argument and equally substantiates our definition of evolution as a proto-cognitive process.

8. An Operational Measure of Information?

In the course of a work that applies some concepts from one science to another, perhaps it is not too ambitious to expect that this application would prove rewarding not only for the research, but also for a better understanding of the applied concepts themselves. This is the case here. The applications of thermodynamic concepts given here seem to enable us to better define the very notion of information, which at present seems to be plagued with confusion.

First, we must face the fact that none of the definitions of information proposed in Sections 2 and 3 distinguishes between "information" and "order". Morowitz (1978) indeed uses the two terms as synonymous. A moment of reflection will show that maximal order can yield zero information in the common sense of the term. An unexposed film is in its maximally ordered state, yet it has no information *about* any object, while its exposure to light makes it less ordered but full of information. Similarly a sentence comprised of strings of the same letter is more ordered than an ordinary sentence, but has practically no information in it. A better distinction is therefore needed between order and information.

A basically similar distinction has been proposed by Yagil (1985) between "order" and "regularity". A regular structure is composed of many repetitive units. In an ordered structure, in contrast, each element is located in a certain, non-random position which is the same in all identical systems, yet the overall pattern is irregular. An example of regularity is a crystal, while numerous examples of order are given by biology, such as the fact that the heart is always found in the left side of the chest. Later the author defines complexity as a special type of order: "An object ... is generally considered as complex if a long list of statements is required in order to describe the position of every ordered element of the object" (p. 4).

The last definition, as is shown below, runs the risk of creating a new confusion, because it does not distinguish between a "complex" system and a merely "disordered" one, both of which require a long list of statements. Nevertheless, the author's first distinction is a sound one, his "regularity" corresponding to my above use of the term "order" and his "order" to

my "information". To avoid linguistic chaos, the definitions proposed here will be used.

So, what is the difference between order and information? The problem has been thoroughly discussed by Gatlin (1972), who pointed out that information can be defined as deviation from a random sequence of signals in two ways: deviation from equiprobability (D_1) and deviation from independence (D_2). These two characteristics have been discussed in detail earlier; see definitions (ii) and (iii) in Section 2. Gatlin stressed that none of these two deviations alone can increase information beyond a certain limit. Consider for example a DNA sequence comprised only of Adenosine: AAAAAAAAAAAA. While the deviation from base equiprobability is maximal here—the probability for A being 1 and for the others 0—there cannot be much information in this sequence. Now consider the sequence ATCGATCGATCG. Here the deviation from equiprobability is zero, but the deviation from independence is maximal. This extreme deviation too is limited in its information capacity. Gatlin's conclusion from these analyses is that information requires a certain optimal mixture of the two deviations.

It is easy to see, however, that both of Gatlin's examples of DNA information are equivalent to the above example of the unexposed film, which has maximal *order* but no information. Her conclusion, therefore, though biologically correct, rests on an unclear distinction between order and information. The above sequences are obviously ordered, but order does not necessarily convey information. Similarly, Hirata (1993), studying the contribution of nutrients, energy and carbon to the D_1 and D_2 measures of ecosystems, denoted them as information. Therefore, a better definition of information is still necessary.

But now another difficulty must be faced. Many authors have lamented the lack of objective measure of the information's value. To quote Brillouin (1956),

> According to our definition, a set of 100 letters selected at random ..., a sentence from a newspaper, a piece of Shakespeare or a theorem of Einstein are given exactly the same information value. In other words, we define "information" as distinct from "knowledge", for which we have no numerical value. (p. 9)

Surely, in principle, these difficulties are not insurmountable. If information is *about* something, it can be measured by some correlation between the message and the system that the message describes. Notice that this correlation can be measured by the same measure of probability used in present information theory, so we need not invent a new formalism. Here our first difficulty, namely, distinguishing information from

order, seems to find a proper solution. If information is *about* a certain system, than, if the system is ordered, the information constitutes an ordered sequence too. Conversely, information about a disordered system must be similarly disordered, but this time we shall not be confused: the disordered sequence is full of information.

The relationship between a system's orderliness and the information describing it is simple. An ordered system can be described by a shorter message than a disordered one. The description of a completely random set of symbols requires the same number of symbols, whereas an ordered sequence can be squeezed into a brief formula.

Information, then, is not order *per se* but an ordered *relation* between a message and a system. To make this definition more quantitative, one would like it to take into account also the physical magnitudes of the two parties. The message "A war broke out" should be shown to contain more information than "a cat sneezed"; surely the different magnitudes of the two events require assigning to each message a different measure of information. Conversely, the size of the message seems to contribute to this measure in a reverse manner. A concise equation describing a physical law is more valuable than a lengthy verbal description.

Can we have all these dimensions of information quantitatively expressed in a single formulation? I believe that the lesson of Maxwell's demon provides a positive answer. Information enables performing a certain work with less effort than that needed to perform the same work without it. We can therefore measure the energy needed to carry out a certain work by utilizing this information, and then measure the energy cost of the same work carried out without using this information; the difference should give a reliable measure for the information. The following measure is therefore proposed. *Information is utilized by an appropriate sequence of operations that enable doing a certain work with a certain amount of energy. Hence, the information value can be measured by the likelihood for the same work to be performed at the same energetic cost by a random sequence of operations.*

Reconsider the examples of biological information mentioned in the previous section to show how this measure can be applied. Recall the gull that exploits alternating winds in order to fly constantly west. It achieves this by a selective sequence of reactions to the winds—letting those that blow west to carry it, landing when opposite winds blow, and making intermediate maneuvers when the winds blow in intermediate directions. The gull uses internal information, i.e. inborn instincts. In order to measure this overall information, one has to calculate the

likelihood that the bird would reach its destination by a merely random sequence of reactions to these alternating winds. Similarly for the lizard maintining a bearable bodily temperature, the question is, What is the probability for the reptile to achieve this goal by haphazardly changing its position during the day and night?

Information can therefore be defined as

$$I = K(\ln P_{W_i} - \ln P_{W_r}), \qquad (34)$$

where P_{W_i} is the probability for the work to be accomplished by utilizing the information, i.e. by a sequence of operations determined by this information, and P_{W_r} is the probability to accomplish the same work by a mere random sequence of operations.

What we have done here is just to modify Brillouin's definition of information, based on the measure of the probability of a static *configuration* of the system's constituent. Our definition measures the probability for a dynamic *interaction* between the system carrying the information and the system about which the information is. This is a purely operational definition, dealing only with the observed utilization of the information and avoiding philosophical queries concerning the nature of the information in itself. I believe its application in the biological context is worth studying.

9. Lamarckianism is Thermodynamically Inefficient

Both forms of evolution, prebiotic and biotic, involve amplification. In the evolution of molecules a microscopic structure gives rise to myriad identical molecules, while the evolution of most present-day organisms, apart from multiplication, also involves the growth of macroscopic bodies. In both cases, amplification leads to a better processing of the microscopic information (Elitzur, 1994b).

Having proposed this trivial formulation, we are in a position to give a new proof for the "central dogma" of modern biology, according to which information can be transferred from one nucleic acid to another, or from a nucleic acid to a protein, but never from a protein to a protein or from a protein to a nucleic acid (Shapiro, 1986). In its general form, this postulate says that the genotype affects the phenotype but never vice versa. This dogma seems to render Darwinian evolution a rather wasteful process that incessantly destroys countless organisms. Lamarckian evolution, in comparison, looks more parsimonious and efficient, fairly rewarding the organism for individual achievements.

A closer examination, however, will lead to the opposite conclusion. *The Darwinian prohibition on inheritance of acquired traits is a simple biological*

manifestation of the Second Law. In order to see how these two principles are basically one, the genotype–phenotype relations will be considered in thermodynamic terms.

Yockey (1992) points out that there are 64 codons in the "source alphabet", namely, DNA and RNA, but only 20 amino acids in the "receiver alphabet" of the proteins. From this discrepancy, he argues, the Central Dogma follows:

> There is more information in DNA than can be translated to protein. Information is discarded in the transmition from mRNA to protein. The discarding of information by any means, including genetic noise, makes the genetic logic operation irreversible because the transition function lacks a single-valued inverse. ... the Central Dogma is a property of any code in which the source alphabet is larger than the destination alphabet. (p. 106)

While this argument is a step in the correct direction, it must be generalized; the Central Dogma must hold even if the "source alphabet" has the same number of symbols as the "receiver alphabet" or even less (as is often the case in other biological processes). The crucial discrepancy between genotype and phenotype is not between the numbers of their letters but between their physical magnitudes, as the following example will show.

Consider a stereophonic tape-recorder playing a recorded symphony, where the tape constitutes the "genotype" while the resulting configuration of sound waves in the air is the "phenotype". If we wish to make a good copy of the symphony, we shall of course copy the tape itself rather than recording the symphony from the air back to the tape. The reason is clear: dissipation considerably decreases the quality of the sound waves arriving at the microphones. In trying to conceive of an ideal recording from the air back to the microphone, we soon realize that this requires a complete reversal of the tape-playing process, i.e. making the sound waves converge back into microphones, placed exactly at the points where the amplifiers were. Such a reversed phenotype–genotype recording allows "Lamarckian" evolution; one can add, for example, another instrument to the played symphony and then record the improved symphony back into the tape. However, in order for such a process to be efficient, exact reversal of dissipative processes is needed, which is far beyond the energy resources of any realistic project.

This example makes, *a fortiori*, any mechanism involving inheritance of acquired qualities impossible. It is hard to imagine, for example, the change occurring ontogenetically in one's finger being copied into the exact site on the DNA molecule where the

instructions for the formation of that finger are. Dawkins' (1989) "bottle-neck" hypothesis is of interest here. He points out that organisms that multiply by a central reproductive systems have an advantage over those multiplying by simply spreading cells from various tissues. According to Dawkins, the former, "bottle-neck" strategy ensures that the genes in all the organism's tissues would co-operate better since they all depend on the success of the central reproductive tissue, thus creating the enormous level of tissue speciation and organization observed in high organisms. This poses a stronger restriction on any mechanism of copying phenotypic changes back into genotypic ones. All changes in all parts of the organism must be recorded on the sme reproductive tissue. Encoding the body's macroscopic information back into the microscopic genes, so that acquired traits would become hereditary, is a process which is bound to give rise to an exponential deterioration of the encoded information, unless there is a perfect reversal of the mechanisms carrying out the genetic instructions.† In comparison, evolution by natural selection is much more reliable and thermodynamically realistic.

Interestingly, Dawkins himself (1987) failed to notice this anti-Lamarckian implication of his observation, and gave a much weaker argument for this purpose. His argument against Lamarckianism is based on the distinction between two embryological theories, namely, preformation and epigenesis. The former theory, long ago disproved, holds that there is a one-to-one correspondence between the DNA molecule and the mature body. In the latter theory, in contrast, the correspondence between the DNA and the body is, to use Dawkins' simile, like the correspondence between a recipe for a cake and the cake itself. There is no correspondence between every word in the recipe and every slice of the cake; if you change "baking powder" for "yeast" in the recipe, the entire cake will change and not only a certain part of it. The organism, Dawkins points out, develops epigenetically, which is an irreversible process, while preformationist development is reversible. Hence, he concedes, it is possible that elsewhere in the universe, another form of life that exhibit preformationist development might be capable of inheritance of acquired traits. The thermodynamic analysis given here, however, shows that even that is impossible. No microscopic infor-

† That such a mechanism is biologically unrealistic is demonstrated by the nervous system. This system faces a similar pair of inverse tasks, namely transmitting information from the CNS to the body and vice versa. Here too, the body does not perform this task by reversing the operation of the same system but by two parallel neural systems, the efferent and the afferent ones.

mation can be copied to the molecular level without costing an enormous price in energy.

Jablonka et al. (1992), in a review defending some forms of inheritance of acquired traits, seem to be aware of these limitations when they point out that such processes can occur only in organisms with late or no segregation between somatic-line and germ-line cells. This way, a local mutation that have occurred, for example, somewhere on a plant's leaf, will not have to be copied back to the seed as a change specific to the leaf, but will be merely transmitted to whatever germs that develop from this leaf. This restriction confines the possibility of Lamarckian evolution to a small and not very interesting number of cases. I still suspect that the above thermodynamic considerations can be applied even against such cases.

10. The Physics of Order-Growth Revisited

This study has so far illuminated two main characteristics of biological development, namely, growth in order, as shown by thermodynamics, and growth in size, as revealed by simple observation. Recent research on the relations between these two processes has led to interesting insights relevant to this study.

Landsberg (1989) and Layzer (1988) have proven that, when a system expands, thereby increasing the number of its microstates, it can exhibit entropy-increase, which is not surprising, *together with an increase of order*. This effect has been suggested first in the cosmological context. It was aimed to account for the ordered state of the universe's beginning by postulating an extremely rapid "inflation" of the universe that added it several new degrees of freedom, while the actual increase of entropy could not have been so rapid. This way, by (11), the difference between the universe's maximal and actual entropies has increased its order.

Can such an effect operate also in biological order-growth? Consider first the physical growth, whether of a population or of a single organism. When this growth occurs too fast, it can leave the entropy growth lagging far behind it. Indeed, such an effect has been encountered when studying the rapid expansion of the population fraction that survived due to an advantageous mutation (Section 5). Notice, however, that the analogy to the above cosmological effect is rather superficial: the new degrees of freedom added to the expanding system do not occur *ex nihilo*, as in the universe's expansion. Rather, the population's expansion takes its full thermodynamic cost by increasing the environment's disorder. At any event, however, a more precise account of biological order-growth obtains: living systems increase their

order by growing in size while maintaining their order.

Brooks *et al.* (1988) pointed out another interaction between size- and order-increase: the constant creation of mutations increases evolution's phase space. Again, these authors propose somewhat misleadingly their formulation as an alternative to the ordinary ways of reconciling entropy and evolution. My objection is that the phase-space expansion they describe clearly takes its ordinary price in entropy. Yet, again, their argument is interesting in itself. What the mutations do, in terms of the earlier formulation of information (9), is to increase the population's *maximal entropy*, hence the operation of natural selection on such a population will increase the difference between S_{max} and S_{act}, thus producing a greater amount of information. To better comprehend this change introduced by mutations, compare a black-and-white film with a color film. The latter, before exposure, is in a more ordered state than the former, as it contains a greater variety of photosensitive chemicals in a state far from equilibrium. Consequently, its maximal entropy is much greater too, as the disorder of coloured patches is greater than that of black and white patches. The film thus owes its information capacity to its initial capability of maximal entropy.

A new mechanism can therefore be pointed out, in accordance with (9), by which evolution succeeds to locally invert the Second Law: *Autocatalysis turns entropy (few mutations in a few organism) into maximal entropy (the possibility that the entire population will constitute a random mixture of mutations). Natural selection prevents the population from reaching this maximal entropy, thereby producing a greater amount of evolutionary information.* Indeed the "Neutral Theory" of evolution (Kimura, 1983) obliges this growth of maximal entropy by the constant "random drift", by which neutral mutants keep appearing and disappearing in any population, unaffected by the environment. This process constitutes an increase of both maximal and actual entropy, but whenever a change occurs in the environment that makes a certain mutation non-neutral, a gap appears between the two entropies, producing new information.

We now arrive at yet another process that links size-growth with information-growth, namely, the merging of two systems. Here we include any merging or interaction between two systems that in some respect renders them one. What happens to the order of such a system? In the biological context the question can be put more specifically: What happens when an organism interacts with another ordered system, such as an ordered environment or another

organism? Here an intriguing consequence of the Second Law is revealed: *The joint order of two systems can be greater than the sum of their separate orders.*

To prove this principle, recall the well-known consequence of the Second Law (Prigogine & Stengers, 1984) according to which the overall entropy of two closed systems after their combination is never less than the sum of their entropies prior to the combination:

$$S_{1+2} \geq (S_1 + S_2). \tag{35}$$

This is due to the fact that the number of the joint system's microstates is multiplicative, and in accordance with the basic rule of probability theory that assigns to a chain of events a probability which is the product of their separate probabilities:

$$P_{1+2} = P_1 P_2. \tag{36}$$

The joint system has therefore many more degrees of freedom than those of the separate systems prior to the combination. One should not be misled by the fact that, in the common formalism, the total entropy of merged systems is only additive, since this is only an arbitrary convenience; logarithms were introduced to eqns (1–3) just in order to make calculations easier (Gatlin, 1972). By definition, these logarithm additions denote a multiplication of the entropies.

Hence, from the above principle an inverse principle logically follows: when two ordered systems merge, and, owing to some reason, *remain ordered*, the probability of the new state decreases according to the above rule. The order of the new system is therefore larger than the sum of the previous orders:

$$O_{1+2} > (O_1 + O_2). \tag{37}$$

This can be demonstrated on (9). It is easy to show that when some systems become one, the two quantities that determine the information quantity of the system, namely, maximal and actual entropy, increase in different rates. Consider two systems possessing the same number of degrees of freedom, say, i microstates. The number of possible microstates in which the system can reside after the merging increases to i^2 and the maximal entropy would be

$$S_{max} = -k \sum P_{i2} \ln P_{i2}. \tag{38}$$

Yet, if the actual entropy of the two systems does not grow to this magnitude—for example, in case they use some (internal or external) energy reservoir to maintain their order—the resulting increase of order can be enormous. A simple example will demonstrate this effect. The sequence 5177274640 is random, taken from a table of random numbers. Yet 51772746405177274640 is far from random, for it

consists of two identical random sequences. The amount of order in each of the sequences in itself was zero, but the joint order is certainly not.

Striking effects of this kind emerge, for instance, every time a coded message is read together with the relevant code: the information content of the combined system becomes far higher than the (nearly zero) sum of the two information quantities before combination. Of course there is nothing miraculous about this sudden gain in order: the two systems, prior to their merging, possessed a high degree of "hidden order" owing to their interaction in the past, and their selection for the combination takes its thermodynamic cost too. It is such hidden order, revealed only upon the interaction of apparently-unrelated systems, that produces some of the most impressive demonstrations of biological ingenuity. For example, an animal's reproductive system reveals its fullest ingenuity only upon the animal's encounter with its mate, and the family that they produce far outweighs the sum of their orders. Ecological dynamics, where populations, species and communities surpass together their separate information capacities (see Elitzur, 1994b), is yet a higher manifestation of this principle. More generally, the interaction between a highly adapted organism and its specific environment, two systems with considerable degrees of order, results in the growth of order that is many times greater than the mere sum of the two separate orders.

Again, Schrödinger's description of the organism as feeding on negative entropy proves mathematically sound: the interaction between environmental and genetic information retrieves enormous amounts of hidden information accumulated in the course of evolution. Similarly, separate units of environmental information, when processed together within the organism, can yield new amounts of information.

The proto-cognitive analogy perfectly holds here too: we achieve a similar sudden information-expansion in our minds every time we bring together two trivial facts and deduce from them a surprising new conclusion.

11. A Critical Review of Current Research and Future Implications

So far this discussion has been restricted to the most fundamental principles underlying biogenesis and evolution, commenting as little as possible on existing models. Now, on the basis of the above discussions, a few comments on other works on

biogenesis are needed. Works pertaining to other issues discussed in this article will also be briefly reviewed.†

11.1. "SUPER-PHYSICAL" BIOLOGY

Any general statement about evolution and biogenesis heavily relies on one's stand-point concerning the relations between biology and physics, briefly referred to in Section 2. It is by no means my intention to enter into this well-worn debate, but it seems appropriate to call attention to a trend in modern science that resorts to almost mystical views of life. It will become clear later that this trend has implicitly influenced also the research on biogenesis.

Miller (1991) has proposed an explicitly animistic model, ascribing living-sentient qualities to inanimate objects and even to atoms. Lima-de-Faria (1988) has put forward a theory of "autoevolution" that denies an evolutionary role to Darwinian selection. Evolution, according to Lima-de-Faria, is an intrinsic force operating in the physical world, biological evolution being only one of its manifestations. Among the evidence he points out to this general evolution, such as mineral crystals resembling animals' horns and skulls, is the striking similarity between the snail's conch and ... the spiral form of galaxies. The author also dismisses the role of genes in the formation of organisms. But nowhere is his ignorance exhibited more embarrassingly than in his discussion of thermodynamics, probability theory and the Second Law. Concerning the latter, Lima-de-Faria "proves" that it is wrong, as biological phenomena involve increase of order. At this point I would prefer to make a positive statement: It is highly instructive that such a misleading discussion of evolution is based on a complete distortion of thermodynamics.

More sophisticated attacks against biology's physical *Weltanschauung* sought to supplement physics with a yet-unknown principle that directs life. Sheldrake's theory (1988) ascribed the formation of organic structures to a yet-unknown, "morphic" field. Benveniste (Davenas *et al.*, 1988) has raised a similar claim in an experiment that attempted to substantiate homeopathy. These works, at least, run the debate on scientific rather than philosophical grounds, as they are testable. The only trouble is that, so far, they have failed to present any reliable experimental evidence. We shall see, however, that the belief in some "living force" has left some traces in the research on the origins of life.

11.2. BIOGENESIS: PHYSICAL LAWS OR "LIVING FORCE"?

During the last few years, the origin of life has become a field of extensive study (Trôan Thanh vôan

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† More general works are reviewed in a consecutive paper (Elitzur, 1994b).

et al., 1992), bubbling with new and original ideas. Until recently, however, the interest in the subject has been scarce and, worse, replete with bizarre ideas. A scientist with the reputation of Fred Hoyle has suggested that life was seeded on earth by an extraterrestrial civilization (Hoyle & Wickramasinge, 1981). A similar theory has been advocated by Crick (1981). These ideas, as Shapiro (1986) points out, differ only little from ancient myths or from creationism, as they merely shift the question mark from one point to another: How was life created on the planet from which it was brought to Earth?

Other theories have proposed more earthly scenarios. They divide into two major trends, namely, "genes first" and "cells first". Models of the former group are due to or stimulated by Eigen's hypothesis (Babloyantz, 1986; Eigen *et al.*, 1981; Schuster, 1991; Eigen, 1992), according to which life began with primitive "genes" that later developed cells containing them. The competing models, most notably Dyson's (1985) and Fox's (1986), argue that the first forms of life were primitive cells, the genetic mechanisms of which evolved only later (see also Ozernyuk *et al.*, 1978; Fleischaker, 1990). While Darwin's casual remark (Section 1) makes him the first advocate of the former school, Oparin (1957), the pioneer theorist of biogenesis, was the founder of the latter. A comprehensive, critical and non-technical review of these models and their variants is given by Shapiro (1986). De Duve (1991), who recently put forward another "genes first" model, also gives a critical and readable review of the field. Lifson (1994*b*) has recently made a critical analysis of these two lines of thought.

The debate between the two schools centers around the question which of the two main characteristics of living organisms, replication or metabolism, was the first to appear in biogenesis. According to the "genes first" school, life has began with autocatalytic molecules, capable of self-replication but not of metabolism, that only later developed auxiliary bodies. In contrast, the "cells first" school argues that life began with the formation of very simple, primordial "cells" that, due to their primitive membranes, were capable of metabolic exchanges with the environment. As absorption of external compounds made them grow, these cells divided, the resulting new cells growing and dividing again in a very primitive form of "reproduction". Exact replication evolved only later, when these cells gradually developed genetic mechanisms of inheritance.

The Minimal Assumption clearly places the present work in the former school, and the discussions so far make the reason clear. In this paper's search for a reasonable scenario of biogenesis, the notion of infor-

mation proved to be of vital importance for explaining the spectacular growth of order exhibited by life. Thermodynamics has made it clear that any local entropy reversal can take place only if the mechanism generating it is supplied with sufficient information about the surrounding conditions. And autocatalysis proved to be the simplest information-processing mechanism that could have evolved by chance, functioning with increasing efficiency. In order to see how awkward is an evolutionary model that does not assume such an information transmission across generations, Dyson's (1985) lucid exposition of his model is closely examined here.

In the beginning, so goes Dyson's account, there were cells that did not replicate but rather split into cells that resembled their parents only crudely by the population of molecules which they contained. The molecules interacted with one another and with molecules that penetrated the primordial cells through their membranes. These cells "might have continued to exist for millions of years, gradually diversifying and refining their metabolic pathways. Amongst other things, they discovered how to synthesize ATP ..." (p. 13)

Against this hypothesis, Lifson (1994) has raised a devastating question: How exactly can non-replicating structures "refine" and "discover"? True, the cells would indeed diversify into many mutants as they split, but in the absence of exact replication, nothing of the parent cells' qualities would survive in the next generation above chance level. Without replication and natural selection, there can be no irreversible changes in the population, no "memory", only minor random fluctuations. Moreover, even if the molecular population of a new cell is somewhat similar to that of the parent cell, the new cell's growth, which requires absorption of new molecules, will considerably dilute the original population. So much, then, for "refinement" of the cells' traits and "discovery" of new ones. If such cells have existed for millions of years, they must have been subject to all perils of the hostile environment without any reliable means of coping with them. Here and there a cell could appear with an advantage for survival, but the offsprings could hardly inherit that advantage, which would vanish together with that cell.

And still, Dyson's account repeatedly refers to purposive processes that develop towards a certain goal, with no mechanism directing these developments, as if matter tends to form life by itself. Clear examples are the third and seventh of the model's ten assumptions:

Assumption 3. Cells do not die and do not interact with one another. There is no Darwinian selection. Evolution

of the population of molecules within a cell proceeds by random drift.

Assumption 7. The active monomers are in active sites where they contribute to the ability of a polymer to act as an enzyme. To act as an enzyme means to catalyze the mutation of other polymers in a selective manner so that the correct species of monomer is chosen preferentially to move into an active site. (pp. 45–6)

Note the words "selective", "correct" and "preferentially". All such characteristics are part and parcel of Darwinian evolution which allows apparently purposive processes as consequences of the strictly causal principles of replication and selection. But once purposive principles are presumed to operate without replication and selection, then the assumption boils down to teleology and "vital force". Lifson (1994) has shown in detail how Dyson's model invokes an evolutionary Maxwell demon that knows what are the "correct" developmental steps without learning them in any physically realistic way. Moreover, by denying the primordial cells the peril of death, Dyson also deprives them of all the advantages of differential reproduction, so simple and yet so important in evolution as we know it. Probably a closer thermodynamic analysis will reveal even more severe difficulties afflicting the presumed functioning of Dyson's primordial cell's membranes. Johnson (1987) has shown that biological membranes face tasks of selection that make them subject to the restrictions posed on Maxwell's demon. For this reason, the development of selective membranes took many generations of Darwinian evolution to reach their present low efficiency, which is nevertheless very high compared to the thermodynamic cost involved. It is unlikely that the membranes of Dyson's cells could selectively absorb chemicals from the environment just by virtue of qualities formed by chance.

The same holds for Fox's (1986) model, according to which life began with "microspheres", i.e. microscopic cell-like structures formed spontaneously by molecules of heat-polymerized amino acids stirred with water. According to Fox (quoted in de Duve, 1991), such microspheres display "lifelike" properties such as growth, budding, division, fusion, catalysis, and even "behavioral" traits such as motility, excitability, communication, and sociality. All these striking characteristics of living systems are believed to appear without exact replication, thereby denying the microspheres Darwinian evolution. Again, this is possible only by violation of the Second Law.

It seems, in general, that an implicit belief underlying all the "cells first" models is that there is an intrinsic principle or law of Nature that directs inanimate matter towards the formation of life. Such teleological principles underly Bergson's and de

Chardin's philosophies. Indeed, de Duve points out that the three main proponents of the "cells-first" models, namely, Oparin, Haldane, and Bernal, were ardent adherents of dialectical materialism, which explicitly assumes an intrinsic tendency of Nature to create higher forms of organization. Dyson (1988) too professes a religious view of the universe. Without entering metaphysical debates, it suffices to point out in the present context that no scientific evidence for a "living force" or any other life-principle has been presented so far. In contrast, the conservative line of investigation, seeking to explain life solely on the basis of the present framework of physics, has proved much more fruitful.

Ozernyuk *et al.* (1978) were probably aware of these difficulties with Oparin's model when they tried the following, somewhat odd line of defense. Based on the interesting findings of their group, namely, Zotin's work on the relations between dissipation and biological complexity (see discussion below), they argued as follows. The smaller the organism, the higher is its respiration intensity, and consequently the higher is the value of its dissipation function, hence the smaller is the probability of the small organism's state. The next argument is that: "Bacteria are the smallest organisms capable of independent existence; therefore the probability of their or similar (in size) living systems' initiation from the primary broth is less than that of the larger organisms" (p. 330). Instead of stopping at this stage to examine carefully this awkward conclusion, the authors proceeded to conclude that Oparin's first cells were not microscopic but huge. They therefore postulated "giant protobionts" that were only poorly ordered.

The slightest disturbance of their dimensions due to mechanical or other causes resulted in a decrease of the probability of the existence of such systems, and they disappeared. However, inside these giant protobionts, smaller living systems might have originated; the latter should have possessed a higher dissipation function. (p. 332)

The fallacies of this reasoning are clear. It extrapolates from *present* living organisms to the primordial forms, ignoring the simple possibility, central to all works on biogenesis, that the first living systems were *both* small and simple. Indeed, in another paper of the same group (Zotin & Konoplev, 1978) the authors explicitly postulate such a gradual emergence of complexity. Notice also that the above scenario renders the protobionts so vulnerable to external changes that it can hardly allow for evolution.

11.3. CHAOS—PHYSICAL AND CONCEPTUAL

The broader physical issue underlying the problem of biogenesis, namely the study of evolution from the

thermodynamic perspective, has, during the last decade, produced a vast and rich literature (Wicken, 1985a, b; Weber et al., 1988, 1989; Brooks et al., 1989; Demetrius, 1992). Many conferences, assembled every year, attest to the growing interest in this subject.

The issue, however, remains highly controversial. Not only have the above works invoked a great deal of criticism, sometimes harsh (e.g. Morowitz, 1986; Ayala, 1989; Volkenstein, 1991), but they often disagreed even with one another. It is especially annoying to note that the literature on the subject still suffers from a great deal of semantic confusion. "Much of the discussion," complains Schneider (1988, p. 130), "is confused because of the ambiguous use of terms." Perhaps this is due to the complexity of the subject, but this is not the only reason. An excessive reliance on mathematical formalism often diverts authors and readers alike from the basic questions, which are, in essence, not too complex. In the preceding discussions an attempt has been made to show that a careful analysis in which jargon complexity is kept at minimum is possible and advisable.

An original approach to the subject has been introduced by the Brussels School (Prigogine, 1955; Prigogine & Stengers, 1984; Babloyantz, 1986). Here again, polemics, often affected by emotional undertones, is lamented by reviewers (Convey & Highfield, 1990). But the basic findings are now widely acknowledged. Many systems were shown to produce striking increase of *macroscopic* order when being driven far from equilibrium. The implications for biology therefore seemed more suggestive than the theories that assume that evolution has began with the formation of microscopic order. However, striking as these patterns of spontaneous order-growth may be, they differ from biological phenomena in a crucial point: they are totally dependent on specific conditions and highly specific energy supply, often returning to disorder once these conditions change. In other words, these artificial systems lack life's ability of *adaptation* to changing conditions. Here again, we need only to recall the distinction made at the beginning of this article between order and information to realize that what is missing in all the models of self-organization: *Information is an ordered relation between a message and a certain reality. Mere order, where the system's constituents display correspondence only with one another, regardless of the environment, is insufficient for the evolution of life.*

Semantic obscurity seems to produce more obscurity, obeying a sad "disorder from disorder" principle. Yockey (1992) has made a devastating criticism of the prevalent uses of the information concept in biology, arguing that all models of biogenesis are equally unsound. It has been shown in detail (Elitzur, 1994a) that Yockey's own use of the relevant concepts is so confused as to render his entire criticism invalid. For example, he dismisses the very relation between "entropy" as used by Shannon and that used in classical thermodynamics. Of course, this is an objection not only against those who apply the information concept to biology but against the very founders of information theory, Brillouin and Shannon. Following Yockey's arguments further, it becomes evident that they are based on a highly idiosyncratic use of the basic thermodynamic terms. He argues, for example, that organized systems are highly entropic, thus rendering all biological development as a *decrease* of order. Many other such awkward confusions abound along Yockey's criticism.

An interdisciplinary field that has prospered during the last decade claims to have far-reaching implications for biological order. This refers to the vast literature on "chaos", made famous by many popular expositions (see Convey & Highfield, 1990). This field deals with non-linear phenomena, where slight changes in the initial conditions alter the system's behavior to an enormous, unpredictable degree. The Lotka–Voltera equation (16), as well as the existence of several positive-feedback mechanisms or, even more so, mixtures of positive and negative ones, often render biological dynamics prone to chaotic instabilities (Robertson, 1991). Here again, priority is due to Darwin (1859), who observed that "the merest trifle would often give the victory to one organic being over another."

Biological common-sense, however—as dubious as this concept may be—suggests that the applicability of chaos theory for the life sciences must be rather limited. For living systems, a crucial dependence on minute details of the initial conditions seem to be the most undesirable thing. Adaptation, by its very nature, exhibits clear reliance on environmental stabilities and regularities. To the extent that stochastic processes take part in evolution, it seems that their role be confined to the limits allowed for the classical concept of entropy. In other words, this role should be the contribution of new variations, later subjected to natural selection.

A few recent works seem to agree with this reasoning. Allen et al. (1993) have shown how chaos is used by living species, surprisingly, to *reduce* the risk of extinction by amplifying the local noise that afflicts local populations. Under natural conditions, several populations of the same species maintain loose connections via migrations. This, together with the resulting asynchrony between the growth-rates of the

populations, prevent extinctions that would have occurred had all populations constituted a single one. This is quite similar to the way that the ordinary random fluctuations are cancelled out [eqn (31)].

Kauffman (1991) has even used the term "antichaos" to denote the stabilities achieved by living systems despite stochastic processes. Indeed, the basis for such antichaotic processes is provided by the very term central to the chaos theory, namely, "attractor", denoting a state to which the system tends to develop and to remain in, regardless of initial conditions. Kauffman shows how such states exert a relatively deterministic influence on the organism's development. It turns out that the relatively few existing cell types that develop through embryonic cell differentiation can be defined as such attractors among the numerous cell types that *could* have developed. This model predicts that a mutation of a single gene would have less harmful consequences on the organism's growth than expected, a prediction confirmed by the data (Kauffman, 1991). The role played in evolution by chaos *per se* is defined by Kauffman as a unique one: evolution gives preference to systems that are poised between order and chaos. This imaginative proposal enables the derivation of many empirical predictions.

Ecology, however, that has been the first biological field to which chaos theory was applied (May, 1974, 1976), remains the most interesting field for such studies (Hanski *et al.*, 1993).

11.4. BIOLOGICAL CHIRALITY

In a research addressing the relation between biogenesis and biological chirality, a very daring hypothesis was proposed to account for the universal chemical handedness of all living forms, mentioned in Section 1. For most scientists, as has been noted, the preference exhibited by all living forms for L-amino acids and D-sugars is due to a mere coincidence in the appearance of the ancestor of all organisms (Eigen, 1992; Shapiro, 1986). In contrast, Kondepudi and co-workers (Kondepudi, 1988; Hegstrom & Kondepudi, 1990) argued that the biomolecular chirality is rooted in a very fundamental asymmetry of Nature, namely, the inherent handedness of the weak force. The authors' reasoning is as follows. Since the weak force has been unified with electromagnetism, one can expect chemical reactions, which are essentially electromagnetic, to show traces of this handedness too. However, the handedness produced by the weak force is so slight that it can hardly be noticed macroscopically. Here Hegstrom & Kondepudi (1990) invoke an interesting scenario:

> For such a small asymmetry to have produced the observed dominance of L-amino acids and D-sugars,

some amplification mechanism must have been operating.

> One of us (Kondepudi) and George W. Nelson ... have shown theoretically that such a mechanism indeed exists in nonequilibrium chemical systems. It is referred to as noise averaging by communication engineers, who exploit it to extract a signal from a noisy background. Imagine a pool of water in which two enantiomers compete with each other, as in Frank's model. Many random influences will tend to favor the survival first of one enantiomer and then of the other. These fluctuations are much larger than the effect of the weak force, but because they are random, they tend to cancel out. Given enough time, the small systematic effect of the weak force will influence the handedness of the symmetry breaking and push the system to a dominance of one enantiomer over the other. (p. 104)

There are more conservative alternatives to this hypothesis (see Avetisov & Goldanskii, 1993), but its reasoning well accords with our scenario. It ascribes to the molecules' population in Darwin's pond the ability to act like an amplifying device, gradually eliminating fluctuations until detecting an extremely subtle effect of Nature. That this scenario has been developed on independent grounds is very suggestive. Kondepudi also reports about computer similations aimed to test this hypothesis. This approach, when applied to other questions related to the origin of life, will no doubt considerably advance the field (see Schuster, 1991).

11.5. A THERMODYNAMIC MEASURE OF TAXONOMIC ORDER?

An interesting series of works sought for a simple, objective thermodynamic measure of the biological degree of organization, independently of specific physiological or evolutionary details. These works are based on the following reasoning: Any biological increase of order must obey the Second Law by increasing the entropy outside the organism, hence heat dissipation should be a reliable criterion for the organism's increase of order. Trincher (1975) has proposed an application of this idea based on von Bertalanffy's equation on the animal's growth:

$$m(t) = \{(m_{fin})^{1/3} - [(m_{fin})^{1/3} - (m_{in})^{1/3}] \, e^{-K't/3}\}^3$$
$$\equiv f(b), \quad (39)$$

where m_{in} and m_{fin} are, respectively, the organism's mass at the initial moment of ontogenesis and its mass at the end of its growth process, and $f(B)$ is the Bertalanffy function that expresses the S shape of the function relating the growing organism's mass to time. From this Trincher obtained the "thermodynamic principle of ontogenetic development":

$$\frac{1}{m} \frac{dQ}{dt} = K \cdot \frac{\ln t}{f(B)} \bigg|_{t_{in}}^{t_{fin}}, \quad (40)$$

where m is the organism's mass and dQ/dt is its rate of heat generation. It follows that the specific heat generation of the animal increases from the moment of the egg's fertilization, assumes an S-shaped rise and reaches maximum value around the end of embryogenesis, slowly decreasing during the animal's growth and reaching a plateau at adulthood. In other words, heat dissipation is directly related to the intensity of internal order-increase. And indeed, this equation is in good agreement with experimental data (Trincher, 1975).

This line of research has been extended to the philogenetic level, similarly based on the premise that "the probability state and the value of external dissipation function specify the degree of the orderliness of the processes proceeding in an open system" (Lamprecht & Zotin,, 1978: 328). Zotin & Zotina (1978) note the following relation between the animal's weight and respiration:

$$\dot{Q}_{O_2} = aW^k, \tag{41}$$

where $\dot{Q}_{O_2}$ denotes the respiration rate, W the animal's weight, and a, k are constants. From this they proceed to show that the larger the animal's weight, the lower its respiration intensity. On the basis of such universal relations Zotin & Konoplev (1978) make a very far-reaching statement:

> It is believed at present that there are no objective criteria of evolutionary progress . . . It is also emphasized that paleontological evidence undoubtedly points to the appearance of more and more perfect [sic] forms of animals and plants . . . Consequently, the question is not about the fact that in the course of evolution the organisms are improved, but there are no reliable criteria of this progress. Such a criterion may be probably developed on the basis of statistical interpretation of the external dissipation function . . . (p. 341)

And indeed, in that paper and in a consecutive one (Konoplev et al., 1978) the authors present data concerning the heat dissipation of animals of various taxonomic groups. They take respiration intensity as an approximation of the external dissipation function, which they hold to be inversely correlated to the system's thermodynamic probability state. A clear agreement seems to emerge between the animal's respiration rate and its evolutionary level, previously determined by other taxonomic methods. This is perhaps not surprising when homeotherms are compared with poikilotherms, as we already know that

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† The authors go as far as to suggest that it is not a coincidence that the exceptions in their tables are "living fossils", i.e. animals that have retained their form during many evolutionary epochs.

‡ In a brilliant control study, Gatlin has demonstrated the same pattern in the progress of children's reading, concluding that this is a universal pattern of information acquistion.

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birds and mammals are more advanced than reptiles and amphibians. It is very interesting, however, that this thermodynamic measure works also within the mammalians: Primata, for example, give the highest dissipation rate while Monotremata and Marsupilia (primitive Australian mammals) give the lowest.†

I am not competent to judge the reliability of these findings, but their far-reaching aspiration should not go unnoticed. The authors claim to present a thermodynamic criterion of orderliness that, independently of all paleontological, biochemical, anatomical and other methods for determining evolutionary relations, gives a very simple measure of orderliness, and hence of evolutionary progress.

Another interesting thermodynamic criterion of evolutionary progress was proposed by Gatlin (1972). Studying the information stored in DNA sequences, she distinguished between two ways by which a system can deviate from randomness and give rise to information. One, D_1, is deviation from equiprobability and the other, D_2, is deviation from independence (these deviations have been briefly explained in definitions (ii) and (iii) in Section 2). This penetrating observation has been discussed in Section 7. Now Gatlin found out that these two deviations from randomness, by which the DNA stores genetic information, also distinguish between two evolutionary levels: Vertebrates have achieved their higher values of information by holding D_1 relatively constant and increasing D_2, whereas lower organisms, whenever they achieved high levels of information, achieved it primarily by increasing D_1. Gatlin concludes that, in the beginning, evolution has proceeded by D_1 increase. This has soon exhausted the genetic code's information capacity, forcing evolution to adopt the strategy of increasing D_2.‡

Gatlin argues that the shift from D_1- to D_2-increase served to increase message fidelity. I would like to propose another reason. As has been shown in Section 7, D_1 and D_2 are measures of order rather than of information. The latter concept denotes a relation between two systems, which might be orderly but are not necessarily so. Gatlin's distinction should therefore be appraised in the light of two questions. Which type of order—D_1 or D_2—is the order we observe in the world in which we live? And which type of order—D_1 or D_2—is manifested in the living organism's structure?

Clearly, the answer to both questions is D_2. Only rarely, natural manifestations of order are of the D_1 type, such as a smooth snow carpet. Even more rare are such biological types of order, such as a completely white fur. Rather, most of the natural regularities are of the D_2 type, i.e. complex patterns in which all constituents depend on one another, and

this is even more notable in biological complexity. The distinction between order and information therefore provides an additional explanation to Gatlin's finding: evolution has shifted from D_1-based to D_2-based information since the latter is better capable of describing environmental order.†

11.6. EVOLUTIONARY EPISTEMOLOGY

The use of the information concept in this work well accords with a new school in philosophy of science that has emerged from works both in biology, behavioral science and philosophy. This school is known as evolutionary epistemology (see Wuketits, 1991 for a review). In Elitzur (1994b) a "generalized biogenetic law" has been proposed, according to which mechanisms that initially operate on the population level are later "internalized" into the individual organism. A novel application has been made of the basic principles outlined in this article to later stages in evolution. The transition from proto-cognitive to cognitive modes of gaining information about the world thus turns to be a particular form of internalization.

12. Summary: What is Life?

All the essential features of life, then, can be summarized within a few concise formulations. Life seems to violate the Second Law, yet it turns out to be the Second Law's very outcome. It is the Second Law that obliges energy sources to radiate outwards rather than vice versa, enabling life to utilize ordered energy currents. It is the Second Law that produces replication errors, e.g. mutations, producing new possibilities of adaptation. And it is the Second Law's ultimate expression that appears in natural selection, whereby organisms decompose, eliminating the noise and giving rise to the environmental information needed for adaptation.

So, in hindsight, when Darwin based his theory on Malthus' observation that for any organism that lives there are numerous ones that perished, he unknowingly pointed out the thermodynamic price paid by evolution to the Second Law. Speaking somewhat poetically, death was shown by Darwin to be one of the chief sculptors of life, the one that removes the redundant pieces of clay. Replacing "death" with "entropy", we may say that entropy does for biological order something similar to that portrayed by the

† Indeed, evolution seems to demonstrate a gradual transition from ordered systems composed of many similar regular or symmetric units, such as a tree's leaves (D_1), to organisms where regularity or symmetry is manifested by the entire body (D_2).

Devil in his reply to Faust's question as to who he was:

Part of nature which always would
Create evil, but always does good.

As a result of this dialectical dynamics, the tasks that the living system faces are highly contradictory. Any organism must be considerably stable, resisting external forces threatening to destroy it, but at the same time, by the very definition of "living", an organism is a *dynamic* system, for which stability seems to be a hindrance. Put differently, the organism must be autonomous in order to preserve itself, yet it must interact with the environment on which it nourishes. The organism must have order, but not the barren, self-correlated order of a crystal; it must be an order in relation to the environment, namely, information. Another conflict stems from the fact that, in order to continuously develop and not fluctuate around the same state, the organism must undergo irreversible changes, but at the same time it must not succumb to the universal irreversibility that leads to lethal equilibrium. Even the organism's dimensions pose a conflict. Life could not begin as something larger than a microscopic system, allowed by probability theory, and even today most organisms are extremely small relatively to their environment. However, the organism needs to obtain information about a macroscopic environment, beyond local, random fluctuations. Life, in essence, always has to navigate between Scylla and Charybdis.

The Minimal Assumption proved to be the most parsimonious one in explaining how this development was made possible. It provides the simplest mechanism capable of transcending these contradictions: life began with the exponential multiplication of a self-replicating molecule. Self-replication has remained the main characteristic of all forms of life. Its exponential growth, and the simple "all-or-none-or-anything" principle of differential survival (Section 6.2) grant evolution several mathematical mechanisms of information-processing: signal measurement, amplification, elimination of noise, etc. But autocatalysis enables evolution not only to receive, process and record signals; it "resets" evolution after any cognitive operation, enabling new signals to be processed.

We have pointed out four major ways by which the Second Law is inverted in processes dominated by self-replication:

(i) Competition between the systems over limited environmental resources leads to a unique, dynamic steady state, where each "action" of entropy, i.e. destruction of some ordered systems, automatically invokes an opposite

"reaction", namely, creation of new systems (Section 5).

(ii) Every interference of entropy in the replication process, for example, the appearance of mutations, increases the populations' *maximal entropy* to which it could evolve. As natural selection does not allow this maximum to be reached, the difference between maximal and actual entropy turns into order (Section 10).

(iii) By spreading a myriad of identical copies over large regions in spacetime, replication surpasses local fluctuations, as opposite fluctuations cancel one another. This enables the population to detect the subtle, invariant regularities dominating huge environments (Section 6.3).

(iv) While replication obeys the Second Law, succumbing to the microscopic errors it inflicts on new copies, it later amplifies these mutations and subjects them to the more stringent macroscopic survival test, whereby most of them are forsaken to the perils of their very originator, the Second Law. Entropy, which usually leads to the irreversible destruction of ordered forms, now irreversibly wipes out the noise of the disordered part in a highly ordered population. The Second Law, regarded by Eddington as the supreme law of nature, is thus fooled by life, enticed against itself!

This triumph over the Second Law by its own consequences is achieved, so we have proved, by life's capability of feeding on information. Information, like order, costs energy. But once achieved, it allows work to be accomplished with much less energy. Once some information is gained and work is done, the energy saved is available for the cheaper gaining of more information, by which, again, more energy is saved, and so on.

As we have shown, life keeps feeding on information, and by the very operation of joining separate units of it, life produces a information that is far greater than the mere sum of the basic units (Section 10). Life, like mind, is capable of gaining insight.

For, whereas the naive mind believes to observe in life the supervision of some supreme thinking, evolutionary theory shows that thinking itself exists in a rudimentary form in any manifestation of life. Which merely shifts the question concerning the source of biological order. For, unlike Maxwell's outlawed demon, life does not create order out of disorder, but rather extracts the existing order hidden beneath the overall disorder. The wonder of life therefore reflects a more fundamental and no smaller mystery, namely,

the fact that the universe seems to have begun in a very ordered form (Elitzur, 1994c). Our body, mind and science are endowed with the ability to retrieve this diminishing universal order. "The most incomprehensible thing about the universe," said Einstein, "is that it is comprehensible."

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