THERMODYNAMICS AND LIFE

by Arthur Peacocke

Abstract. The basic features of thermodynamics as the "science of the possible" are outlined with a special emphasis on the role of the concept of entropy as a measure of irreversibility in natural processes and its relation to "order," precisely defined. Natural processes may lead to an increase in complexity, and this concept has a subtle relationship to those of order, organization, and information. These concepts are analyzed with respect to their relation to biological evolution, together with other ways of attempting to quantify it. Thermodynamic interpretations of evolution are described and critically compared, and the significance of dissipative structures, of "order through fluctuations," is emphasized in relation both to the evolutionary succession of temporarily stable forms and to kinetic mechanisms producing new patterns.

> All kinds of private metaphysics and theology have grown like weeds in the garden of thermodynamics.
> (Hiebert 1966, 1075)

This pungent judgment of a distinguished historian of science serves to remind us that, although thermodynamics has an austere and lofty intellectual and architectonic framework, it has nevertheless frequently generated a plethora of often gloomy emotions in those who have attempted to apply it on a cosmic scale. The noble peroration of Bertrand Russell ([1903] 1963, 41) urging "unyielding despair" upon mankind as he contemplates the demise of all its achievements "beneath the debris of a universe in ruins," as the second law of thermodynamics pronounces the inevitable heat-death of the cosmos, is matched even by the cooler head of the founder of cybernetics, the mathematician Norbert Wiener:

> We are swimming upstream against a great torrent of disorganization, which tends to reduce everything to the heat-death of equilibrium and sameness

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> described in the second law of thermodynamics. What Maxwell, Botzmann and Gibbs meant by this heat-death in physics has a counterpart in the ethics of Kierkegaard, who pointed out that we live in a chaotic moral universe. In this, our main obligation is to establish arbitrary enclaves of order and system. These enclaves will not remain there indefinitely by any momentum of their own after we have established them.... We are not fighting for a definitive victory in the indefinite future. It is the greatest possible victory to be, to continue to be, and to have been. No defeat can deprive us of the success of having existed for some moment of time in a universe that seems indifferent to us (Wiener 1956, 325).

Here we have echoes, too, of Jacques Monod's "the ancient covenant is in pieces; man at last knows that he is alone in the unfeeling immensity of the universe out of which he emerged only by chance" (Monod 1972, 167).

What, in fact, is this aspect of modern physics and physical chemistry to which is attributed such dire consequences? Harold MacMillan, the former Prime Minister of Great Britain, wrote a book about politics a few years ago which he called *The Art of the Possible*; thermodynamics is the *science* of the possible—it stands in relation to science as a whole very much like logic does to philosophy. It does not invent; it proscribes. Paradoxically, classical thermodynamics has been most successful in deriving the relationships that characterize physical systems at equilibrium, that is, just those systems in which all processes are reversible, unlike most actual systems which always involve natural irreversible processes. The state of equilibrium is that to which all processes tend to lead any actual system. So classical thermodynamics deals accurately and powerfully with a kind of limiting world—that to which the actual tends. It is not, on that account, to be underestimated. It was, for example, by purely thermodynamic arguments that Max Planck, thinking about the observed features of the equilibrium between matter and radiation, in the famous "black body" problem, came to the heretical and impossible conclusion that energy was exchanged in discrete units ("quanta") and not continuously; more recently it has been by the application of thermodynamics to black holes that Stephen Hawking at Cambridge University has been able to make a start on that ultimate goal of physics, a unified field theory; and, more modestly and pedagogically, I myself recall the astonishment with which I, as a chemistry student, realized that classical thermodynamics allows, from purely thermal measurement (heat capacities, heats of transitions and reaction), the calculation of the equilibrium composition of a chemical reaction mixture at *all* temperatures, given the measurement of the equilibrium constant at *one* temperature (and this latter can itself be calculated by statistical thermodynamics from spectroscopic data in certain cases). So the thermodynamic account of equilibrium and its interpretation of natural processes (which we shall come to later) may be regarded as one of the best established pillars of modern science.

The edifice of classical equilibrium thermodynamics has rightly been likened by G. N. Lewis and M. Randall to that of a medieval cathedral, through which, in their own classic and pellucid exposition, they conceived of themselves as conducting their readers:

> There are ancient cathedrals which, apart from their consecrated purpose, inspire solemnity and awe. Even the curious visitor speaks of serious things, with hushed voice, and as each whisper reverberates through the vaulted nave, the returning echo seems to bear a message of mystery. The labor of generations of architects and artisans has been forgotten, the scaffolding erected for their toil has long since been removed, their mistakes have been erased, or have become hidden by the dust of centuries. Seeing only the perfection of the completed whole, we are impressed as by some superhuman agency. But sometimes we enter such an edifice that is still partly under construction; then the sound of hammers, the reek of tobacco, the trivial jests bandied from workman to workman, enable us to realize that these great structures are but the result of giving to ordinary human effort a direction and a purpose.
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> Science has its cathedrals, built by the efforts of a few architects and of many workers. In these loftier monuments of scientific thought a tradition has arisen whereby the friendly usages of colloquial speech give way to a certain severity and formality. While this may sometimes promote precise thinking, it more often results in the intimidation of the neophyte. Therefore we have attempted, while conducting the reader through the classic edifice of thermodynamics, into the workshops where construction is now in progress, to temper the customary severity of the science in so far as is compatible with clarity of thought (Lewis and Randall 1923, vii).

But, since that was written, the workmen have been brought in again, this time to work on irreversible processes and dissipative systems, indeed those very aspects which are pertinent to living systems. Thus thermodynamics continues to develop and the reek of tobacco is still to be discerned—not to mention the jests of the workmen!

THE BASIC FEATURES OF THERMODYNAMICS

In its classical form, as developed in the nineteenth century culminating in J. Willard Gibbs's great monograph on "The Equilibrium of Heterogeneous Substances" (1876; 1928), thermodynamics operated with a "black box" and phenomenological approach in which exchanges of matter, heat, and other forms of energy were related to macroscopic properties (pressure, temperature, volume, etc.) of the system in question. It referred to matter in bulk (note that pressure and temperature have no meaning for only one or a few molecules). The *state* of a system (macroscopic state) is determined by its *properties* just insofar as these properties can be investigated directly or indirectly by experiment. As Gibbs puts it: "So when gases of different kinds are mixed, if we ask what changes in external bodies are necessary to bring the system to its original state, we do not mean a state in which each particle shall occupy more or less exactly the same position as at some previous epoch, but only a state which shall be undistinguishable from the previous one in its sensible properties. It is to states of systems thus incompletely defined that the problems of thermodynamics relate" (1876, 228). The properties of a substance describe its present state and do not give a record of its previous history. So when a system is considered in two different states, the difference in volume or in any other property between the two states depends solely upon those states themselves and not upon the manner in which the system may pass from one state to the other. Furthermore, classical thermodynamics distinguished between "extensive properties," dependent on the amount of matter in the system (e.g., volume), and "intensive properties," not so dependent (e.g., temperature, pressure, density, composition). The values of the parameters that denote these properties are characteristic of the system in a given state—that is, they are "properties of the state of a system"—and, if the system changes from, say, state A to state B, each of these properties changes by a definite amount (e.g., volume $V_A \rightarrow V_B$, i.e., by $(V_B - V_A) = \Delta V$, where Δ represents a positive increase in the value of that parameter), regardless of what the intervening states may be *en route*. Because of this, properties of the state of a system can be related mathematically, at least in principle, and their concomitant variation handled by the differential and integral calculus. A Zeroth law underlies the whole edifice, to the effect that if two systems are in thermal equilibrium with a third system then they are in equilibrium with each other. All systems in such mutual thermal equilibrium are said to have the same temperature, an absolute scale of which it is one of the purposes of the exercise to devise. Systems not in thermal equilibrium are said to have different temperatures.

The *first law* of thermodynamics is simply the formalization of what is more familiar as the law of conservation of energy, which simply affirms that an entity, energy, has many forms (thermal, electrical, mechanical ["work"], etc.) which are interchangeable with conservation of its total amount. More formally, this issues in the assertion that there exists a property of the state of the system, called the internal energy (U or E), such that changes in this property are the sum of the heat absorbed by the system and the mechanical work done on it during any change of state (when only these two forms of energy are involved). Subsequently, to involve the quantity $U(E)$ in equations characteristic of the state of the system and to apply the calculus to it with respect to any changes it may undergo is then equivalent to assuming the first law without any further ado.

The *second law* of thermodynamics is more elusive and multiple in its expression and formulations. It is concerned with the unidirectional nature of our experience—dropped eggs do not reassemble and fly back into our hands and we cannot refill the petrol tanks of our cars by pushing them backwards! There is a universal tendency for work, and all forms of energy convertible to work, to degenerate into uniform thermal energy (e.g., in any mechanical device, some of the original energy always goes to thermal energy, heat, from friction). All real processes are unidirectional and, although local changes can be reversed at the expense of irreversible processes elsewhere, no real process is ever reversible in its entirety.

Notice immediately the special role of heat (thermal energy) as that form of energy least available for conversion into directed mechanical work. The earlier developments in the nineteenth century involved the formulation of how much of the heat contained in a body could be converted into work and how the efficiency of this conversion was related to a temperature scale. Another concern arose from the recognition that degrees of irreversibility in natural processes needed to be quantitatively compared. The ideal, or fully reversible, process was taken as the baseline, and so to represent a process manifesting minimum irreversibility. Hence the change in the quantity S, the "entropy," which was postulated to measure degrees of irreversibility, was assigned a zero value for such ideal processes (dS, or $\Delta S = 0$). Careful analysis of the relationships between heat, work, and temperature both in natural, irreversibly operating and in ideal, maximally efficient, reversibly operating heat engines showed that the property S could be a "property of the state of the system" if it was equated, for reversible processes, to the ratio of heat absorbed reversibly divided by the temperature. By definition it remains unchanged in reversible, adiabatic processes and increases in natural, irreversible processes in an isolated system (no heat or matter exchange occurs across its boundaries). Since natural processes always tend to a state of equilibrium, it follows that the entropy of an isolated system reaches its maximum when that system reaches internal equilibrium.

Because this analysis, one of the great achievements of nineteenth-century science, led to the formulation of a property, the entropy (S), that not only measured the extent of irreversibility in a natural process in a particular system but was also a property of the state of that same system, the quantity S could be related to other properties of the state of the system—such as internal energy (U), pressure (P), volume (V), temperature (T), composition—and changes in it could be handled by the calculus, as for those other properties.[1] The second law could then be stated in the form: "In any real process, there is always an increase in entropy." The greater the value of the increase in entropy (ΔS) in a natural process occurring in a particular system, the greater the extent of its irreversibility, that is, the more "degraded" and less available for performing mechanical work had the energy become in the process, and the more it had become chaotic, thermal energy. Thus changes in entropy measured something to do with the "character," not simply the quantity of energy, in a system.

What this character was, that was related to availability to perform directed mechanical work, only became clear with the later development of statistical thermodynamics, particularly at the hands of L. Boltzmann. This development is most easily understood in the context of the realization that the energy states of any system are all discrete and not continuous (even for translational energy). The characteristic of the energy that is related to the entropy was proposed by Boltzmann to be the "spread" or distribution of matter over the possible available energy states—the degree of randomness or disorderliness, as it were, of the matter-energy distribution. To be more precise, the entropy (S) is related to a quantity, denoted as W, which is the number of complexions of the system, that is, the number of possible dispositions of matter over the (equiprobable) available energy states or, more precisely, the number of *micro*states corresponding to a given *macro*state identified through its macroscopic properties. The Boltzmann relation was simply

$$S = k_B \ln W$$

where k_B = the Boltzmann constant and is the gas constant (R)/Avogadro's number (N_0); and the logarithm is a natural one, to exponential base e. Note that $W = 1$ represents a maximum state of order in this respect, with minimum entropy, namely zero, since $\ln 1 = 0$.

Disorderliness is, in this context, the zero value of a variable, orderliness, which is the extent to which "any actual specimen of an entity approximates to the 'ideal' or pattern against which it is compared" (Denbigh 1975). Such orderliness reaches its maximum extent in the "state of order" which is "an ideal reference state, laid down and specified, according to certain rules or conventions, which is taken as having 100% orderliness" (Denbigh 1975). This state of order might well be the geometrical order of a crystal lattice at absolute zero, and orderliness would decrease (i.e., disorderliness would increase) according to the extent to which the atoms or molecules of the crystal were displaced from the lattice points and/or the extent of the spread of its quantized energy states relative to the ground state. For populations rather than single entities, 100% order with respect to any parameter or property would be characterized by all the members of the population exhibiting the same value of that parameter, or the same property. So when, loosely, entropy is said to be a measure of disorder or randomness, it is this kind of orderliness that is being referred to. It is, to use an example of Kenneth Denbigh, the kind of order exemplified by a perfect wallpaper pattern rather than that of an original painting. Such "order" is therefore scarcely adequate as a measure of the complexity and *organization* of biological systems. Nevertheless it could be affirmed that the kind of *dis*order measured by entropy is incompatible with biological complexity and organization and, indeed, the state of maximum entropy, of maximum disorder in the sense defined, is equivalent to biological death. Thus we may say that a state of low entropy is a necessary but not sufficient condition for biological complexity and organization to occur.

Note that the above equation could have been written as

$$- S = k_B \ln (1/W),$$

in which case increase in the "negentropy" ($- S$) could be regarded as parallel to an increase in order measured by ($1/W$). This way of speaking was popularized by E. Schrodinger (1944), but in my view it is unnecessarily obfuscating, especially if an increase in order does not necessarily entail an increase in biological complexity and organization.

EVOLUTION AND THERMODYNAMICS—THE PROBLEM

One of the implications of the classical thermodynamic account of natural processes, just outlined, is that time has, in relation to natural events, a unidirectional character so that entropy has often been called "time's arrow," for the increase in entropy displayed by natural processes apparently specifies (or, better, is closely linked conceptually with) the direction of the flow of time. All this has a curious and apparently problematic relation with that other great scientific development of the nineteenth century—namely the discovery of time in biology, more precisely, the idea of biological evolution. Time had already been discovered in the eighteenth century in the sense that the development of geology as a science had vastly extended the time-scale of the history of the earth as a planet and of the living organisms, including man, upon it. Then, with Charles Darwin and Alfred Wallace and the activity their proposal engendered, an understanding of both the interconnectedness of all living forms and of their progressive development from single cells (themselves not so simple) to more and more complex forms was surprisingly rapidly established, in spite of the opposition about which we all know. Yet, according to one version of the laws of thermodynamics, "the energy of the universe is constant; the entropy of the universe is increasing to a maximum" (Clausius

1865, 353). As we saw, entropy, and so disorder in the sense we have defined, increases in all natural processes. So how is it that living organisms can come into existence and survive, swimming, as it were, against the entropic stream carrying all to thermal equilibrium and heat-death? In living organisms, we see natural objects in which, while they are alive, complex organization is being maintained and even enhanced against the universal tendency of all processes to occur with an overall increase in disorder.

Are living organisms actually, in some way, breaking the second law of thermodynamics by maintaining systems in a high state of organization and so a low state of disorder, of low entropy? The brief answer to this question is "No," when one recalls that for a natural process or change one must take into account everything that changes. Now living organisms are *open* systems exchanging energy and matter with their surroundings, and the changes in entropy in both the organism and the surroundings have to be assessed. So it is perfectly possible for there to be a *decrease* in entropy associated with the processes of metabolism, and so forth, occurring in a living organism while at the same time this decrease is more than offset by an *increase* in the entropy of the surroundings of the organism on account of the heat that passes to these surroundings from the organism (recall the basic classical definition of entropy increase as heat absorbed divided by temperature, for a reversible process). So living organisms, once in existence, do not in any sense break the second law of thermodynamics—any more than these laws are broken in certain purely physical processes when a more ordered form of a system is generated with the evolution of heat, for example, the freezing of super-cooled water to form ice or the generation of a density gradient in the molecular concentration along a tube of gas which is in contact with a source of heat at one end of the tube and a sink for heat at the other end. In such systems a steady state is eventually reached with respect to the throughput of heat and the distribution of the molecules, and in this state there is both energy flow and a steady rate of production of entropy in the flow processes. In these physical samples it is, of course, an ordering that is occurring at the expense of a disordering (equivalent to an increase in entropy) of the surroundings; it is not strictly an increase in organization of the kind required to maintain living systems. But at least an increase in order, thus physically defined à la Boltzmann, is a necessary prerequisite, if not a sufficient one, for the maintenance of biological organization.

But it also has to be recognized (Wicken 1978) that there are some natural processes, in which there is an overall increase in entropy, which nevertheless manifest an increase in molecular complexity of a kind not simply captured by the simple concept of order already defined. Molecular complexity *can* increase in chemical reactions that involve association to more complex molecular forms, in full accordance with the second law. For any decrease in entropy that results from the decrease in the number of complexions (*W*, above) when atoms or molecules combine, that is consequent upon the loss of translational modes of molecular motion, with their closely packed energy levels, to (by and large) vibrational modes, with their more widely spaced levels, is offset (i) by an increase in the entropy of the surroundings resulting from the heat generated by a decrease during the chemical combination in the potential (electronic) energy of chemical bonds and (ii) by an increase in entropy due to the increase in configurational possibilities that occur, in spite of a reduction in the number of molecules, when there is an increase in molecular heterogeneity with the formation of new chemical species (and this contribution is greater the greater the number of possible new chemical structures).

Jeffrey Wicken (1978; 1979; 1980) denotes (i) and (ii), respectively, as "energy-randomization" and "matter-randomization" to emphasize that it is the randomizing tendencies formalized by the second law of thermodynamics that drive forward the formation of more complex structures. The earth's biosphere is in a steady state of free energy flux, from the sun to the earth (with its biosphere) to outer space, with the rhythm of the earth's diurnal rotation. Within the biosphere itself there is a continuous steady flow of energy through the various trophic levels of ecosystems, with concomitant transfer of heat to the nonliving environment and so to outer space (Morowitz 1968; 1974).

The formation of chemical bonds by process (i) then, entirely in accord with the second law and in conjunction with (ii), provides the opportunity for the increase in molecular, and so organizational, complexity upon which natural selection then operates. Wicken (1980) has further argued that, for these reasons, the biosphere must evolve toward a stationary state of maximal structuring and minimal dissipation with respect to the (solar) applied free energy gradient. Wicken's general argument I have expressed here in terms of entropy rather than in his terms which are those of "information," by which he means simply the negative of entropy as thermodynamically and statistically defined (see below), and so related to order in the strict sense (and not to organization). So the second law of thermodynamics, far from prohibiting any increase in complexity, necessitates its increase at the molecular level. But does the recognition of this provide any thermodynamic basis for the actual coming into existence in the first place of living, organized systems of matter, as distinct from providing an interpretation of their continued existence, growth, and death?

In the first half of the twentieth century, classical thermodynamics had been extended to natural irreversible processes at the hands of Lars Onsager, J. Meixner, A. Katchalsky, S. R. de Groot, Theophile de

Donder, and Ilya Prigogine and his colleagues of the Brussels school. Although this extension reaped many rewards in other fields, it did not assist much in the interpretation of biological processes. For the thermodynamics of irreversible processes was developed for situations in which the flows and rates of the processes were linear functions of the "forces" (temperature, concentration, chemical potential gradients) that impelled them. Such linear, nonequilibrium processes can, as we just saw, lead to the formation of configurations of lower entropy and higher order—so that nonequilibrium can be a source of order. But the order so created is not really structural and is far from the organized intricacies of biology. Moreover, and more pertinently, biological processes depend ultimately on biochemical ones and these, like all chemical reactions not at equilibrium, are intrinsically nonlinear (in the relation between reaction rates and driving forces, the "affinity," or free-energy difference). Thus they fell outside the scope of irreversible thermodynamics at this stage of its development.

To show that the Boltzmann equilibrium ordering principle (coupled with exp $[-E/k_B T]$ being proportional to the probability of occupation of a state of energy E at temperature T) is inadequate to explain the origin of biological structures, it suffices to take an example of Manfred Eigen (1971a). Consider a protein chain of 100 amino acids, of which there are 20 kinds—and biological systems are orders of magnitude more complex than this. The number of permutations of the possible order of amino acids in such a protein, on which its biological activity and function depend, is $20^{100} \hat{=} 10^{130}$, assuming all sequences are equally probable. This is the number of permutations necessary to obtain a given arrangement starting from an arbitrary initial distribution. If a change of structure occurred at the (impossibly) high rate of one every 10^{-8} seconds, then 100^{122} seconds would be needed altogether to produce a given sequence; yet, the age of the earth is 10^{17} seconds. So the chance of spontaneous formation of the protein, à la Boltzmann, through processes at equilibrium, is indeed negligible. Equilibrium cannot give rise to biological order. There is no chance of an increase in order of the Boltzmann kind by equilibrium considerations.

However, account now has to be taken of the earth not being a system in equilibrium but being, and always to have been, an *open* system through which there is a major flux of energy inwards from the sun and outwards into space (and perhaps some minor flux of matter, too, although this seems in practice to be negligible). Thus, at present, the earth receives energy from the sun during the day and absorbs this heat both physically and chemically through the green chlorophyll of plants; at nighttime much of this energy is radiated out again, but some is stored in the carbohydrates of plants and so finds its way into other living organisms (including ourselves) as the intermediate source of their energy before again being given up as heat to the atmosphere and so to space. Hence biological evolution has to be considered thermodynamically in relation to the openness of this whole system and, in particular, of the biosphere located near to and on the earth's surface. So it will be a thermodynamics of natural, irreversible processes in open systems that will be relevant to biological evolution and the coming into existence of living systems. Before we consider developments in this respect, which neatly complement the considerations abvanced above concerning the thermodynamic basis for the generation of molecular complexity, it is important to look at a number of other approaches to quantifying the evolutionary process. These approaches have often been intricately interwoven in discussions of the relation of thermodynamics to the evolutionary process, and it is essential to be clear about the relevant concepts involved. The next section expounds the most significant of these. From the viewpoint of this article it is the concepts of complexity and organization that are the most pertinent, and their relation to the thermodynamic interpretations of evolution are considered in the section after next, to which the reader may proceed directly, if so desired, to follow the general direction of the argument.

WAYS OF QUANTIFYING BIOLOGICAL EVOLUTION

In this section the question is addressed: Can one devise any nonthermodynamically defined quantities that will characterize biological evolution and will undergo a monotonic change (increase or decrease) with time?

Order. The quantity W or the "number of complexions" of a system—the number of microstates, in relation to the distribution of energy over the available energy levels of the matter in the system, that corresponds to a given macrostate—may be defined independently of its relation to entropy in the Boltzmann relation. As W increases, the spread of energy over the available states increases and, intuitively, this can be regarded as cognate to an increase in disorder, so that $1/W$ may be regarded as a measure of order in this sense. It is pertinent to ask if the order, defined as $1/W$, of *living* systems can be said to increase during evolution. However, on this scale the maximum degree of order is that of the perfect crystal at the absolute zero (leaving out zero-point energy considerations for the moment, relevant to the third law of thermodynamics); for such a system $W = 1$, the disorder is minimal (zero, by the Boltzmann relation) and order, so defined, is maximal.

Clearly evolution cannot be regarded as the development of living systems towards the point of exhibiting the order of a perfect crystal! Indeed, this is precisely why we had to refer to complexity and organization as characterizing living systems rather than to this more formal kind of order. Since entropy *is* related to order, or rather disorder W, by the Boltzmann relation, no easy generalizations concerning the relation of evolution to entropy as such are likely to be forthcoming.

Information. Closely related to the use of entropy as a measure of disorder is the communication theory concept of information (I), which may be defined as

$$I = k' \frac{1}{\ln 2} \ln Z_0 = k' \log_2 Z_0,$$

where k' = positive constant; I = the information content (in "bits") of one outcome or case selected out of Z_0 possible outcomes or cases (if the Z_0 possible outcomes or cases are interpreted as the Z_0 possible complexions of a physical system of which the actual macroscopic state of the system is one). Information (I) so defined may be regarded as the gap in our knowledge of a system that needs to be filled to pass from knowledge of the macrovariables (P, V, T, etc.), characterizing its macrostate as a whole, to knowledge of the values of the microvariables that would specify every microstate with respect to the distribution of energy over the available states of the matter in that system. Such information (and this is even more apparent in C. E. Shannon's definition of information [H] in another equation that is parallel to an alternative definition of entropy) represents the missing information we need in order to describe completely a natural system: so it could be thought to measure the complexity, seen then as a negative quantity. This implies the existence of a channel of communication between observer and system. A system, on this view, appears complex when we do not know enough to specify it completely, even though we know enough to recognize it as a system. H. Atlan has expressed this informational definition in the following way: "Complexity is a negative quantity which measures our ignorance about the organization of a natural (i.e., non-man-made) system [about] which we know enough, however, to recognise it as an entity and to enumerate its constitutive parts" (Atlan 1978, 177).

There is clearly a parallel between the equations for entropy and information. So an increase in the disorderliness and entropy (S) of a system has often been regarded as equivalent to a decrease in information (I, or Shannon's H) of the system, that is, to an increase in our lack of information or knowledge of it. Conversely, a decrease in entropy has been regarded as parallel not only to an increase in orderliness, as already defined, but also to an increase in information content. That is, $S = -I$ or, more precisely, $\Delta S = -\Delta I$, *where* Δ stands for a positive increase in a quantity.

The applicability of these ideas to biological systems has been widely discussed since their original formulation (Shannon and Weaver [1949] 1962; Quastler 1953; Brillouin [1956] 1962), but this application has proved to be controversial (Apter and Wolpert 1965)—even involving disputes about the actual signs (+ or −) of the relation between entropy and information (Wilson 1968). This is not surprising, for the correlations between information and entropy and between information and disorderliness are only possible in situations where *information* can have a clearly defined meaning (as it can in relation, e.g., to the genetic code), and precise delineation of, for example, whether the system is being observed from within or without has sometimes been lacking (Atlan 1978, 177).

A number of authors, indeed, firmly deny that any equivalence between information and thermodynamic entropy has been proved (Ferracin, Panischelli, Benassi, di Nallo, and Steindler 1978). The difficulty arises particularly in applying the concept of information where new information is being generated and the system is also subject to disorganizing effects from outside, that is, to "noise." Can the concept of information cope with such characteristically biological problems as the development and evolution of the functional, rather than purely spatial, order of biological systems? M. J. Apter and L. Wolpert (1965) concluded "that attempts to apply information theory to development have been either faulty, meaningless, or trivial." One recalls, in this context, the stress of Eigen (1971) on the need for some independent criterion of valuation of new macromolecules in an evolving system: for the generation of functional orderliness depends on kinetic and stochastic considerations (amplification of fluctuations, etc.) for which the unmodified concept of information seems inadequate. Another way of involving information in a criterion of evolutionary change has been developed by Atlan and will be discussed later (subsection on "Organization" below).

Fitness. It is widely agreed that natural selection of living organisms is an important mechanism of evolutionary change—probably *the* mechanism since other contenders have a penchant for disappearing from the scientific scene. So it has been widely assumed that this implies that there has been an increase in a quantifiable parameter called "fitness" throughout evolution (cf., Fisher 1930). Yet no satisfactory definition of a fitness that constantly increases in evolution has ever been forthcoming (Ho and Saunders 1979), first, because natural selection does not define such a quantity which increases in every evolutionary change (a mutant organism can often supplant the original strain by occupying a new biological niche and not by direct competition), and, second, because it is not possible to order existing species by fitness (e.g., In what sense may, say, a man be said to be fitter than, say, a protozoan?). And is not one here dangerously near to that vulnerable reduction of the neo-Darwinist interpretation of evolution to the tautology that it is the fittest that survive, with survival as the criterion of what is fit?

Furthermore, fitness is not so much a property or characteristic of a particular kind of organism in itself (whether its homeostatic ability, its efficiency in use of limited resources, or its general energy and level of maintenance of vital processes) but rather a relation of that organism to the external world, more like a potential in thermodynamic or electrical theory. In which case, would it not be more pertinent to focus on a "gradient of fitness" (by analogy to the gradient of a potential as being equal to a force) as being the driving force in evolution, that is, to make the relevant quantity the rate of change of fitness, in a particular local situation or in a particular putative evolutionary change, with respect to some parameter of the change itself (e.g., time)? This would recognize that indeed *local* increases in fitness do occur, but it would not imply any general increase in fitness throughout evolution that gives the latter its direction (for a fuller discussion see Ho and Saunders 1974). Note that, in all of this, the importance of fitness is not denied—only its usefulness as a parameter of evolution.

Complexity. If behavior is included along with structure and function as a feature of living organisms that contribute to its "complexity," then it is fairly safe to assert that there has, by and large, been a general increase in complexity during the broad sweep of the evolutionary process. There is a sense in which a dog is more complex than an amoeba and we are more complex than dogs, if you include our behavior and brains. The human brain, with its 10^{11} nerve cells each fed by and feeding into hundreds or thousands of neurons, and making contact through $\sim 10^{14}$ synapses, is apparently the most complex piece of matter in our known universe (Hubel 1979). But, having acknowledged that, one still has to ask if complexity can be defined so as to yield a more finely tuned discrimination between different stages of evolution. The question is given some edge by the tendency of some authors, notably Pierre Teilhard de Chardin, to associate an increase in complexity with an increase in consciousness, his so-called law of complexity-consciousness (cf., Towers 1966, 32).[2] Be that as it may, there is clearly a need for more precision in our attribution of complexity to living organisms. This complexity can be regarded as a level within a whole formalized hierarchy of complex systems, and this has been elaborated in immense detail and with multiple cross-comparisons in that tour de force of systems theory, J. G. Miller's *Living Systems* (1978). This far-ranging attempt to subsume systems ranging from the cell up to supranational systems under one classificatory scheme does at least have the virtue of making clearer just how complex living systems are. He postulates a "generalized living system interacting and intercommunicating with two others in its environment," which consists of nineteen critical subsystems essential to life: two which process both matter-energy and information, eight which process matter-energy, and nine which process information. These subdivisions are identified and cross-compared with each other in each of the seven levels in what he regards as the natural hierarchy of complexity, namely, cell, organ, organism, group (of organisms), organization (within the group), society, and supranational system.

Miller has chosen these seven systems as reference levels since each of them is living, that is, is a self-reproducing organized complex; but a molecular biologist would include lower nonliving entities in the biological hierarchy and would perhaps more naturally think of a sequence such as atom-molecule-macromolecule-subcellular organelle-living cell-mutlicellular functioning organ-whole living organisms-a population of organisms-ecosystem (e.g., Gerard 1957). Each successive member of this series is a single whole constituted by parts which are the preceding members; the wholes are "organized systems of dynamically interrelated parts" (Nagel 1952). (It is common in speaking of such a series to to refer to the first and less complex, as in the sequence above, as "lower" and the more complex as "higher" without any value judgement being implied by such a description.) H. A. Simon (1962) has affirmed that natural, especially living, hierarchies are, more often than not, "nearly decomposable"—that is, the interactions among subsystems (the "parts") are relatively weak compared with the interactions within the subsystems, a property which simplifies their behavior and description. With this in mind W. C. Wimsatt (1976) has been able to distinguish further between what he calls "descriptive complexity" and "interactional complexity" and, in parallel, between "descriptive simplicity" and "interactional simplicity." He argues that all systems, including living ones, can be viewed from a number of different perspectives which may yield several different, nonisomorphic "decompositions" of the system into parts (following Kauffman [1971]).

Each of these different theoretical perspectives (which could include among other things physical properties, chemical constituents, [bio]-

chemical reactions, cell types, physiological systems, etc.) suggests criteria for the identification and individuation of the parts, that is, for "decomposition" of the system into thus-defined parts; and the criteria are different for each of the theoretical perspectives. If all of a set of such decompositions of a system produce coincident boundaries for all parts of the system, then the latter is called *descriptively simple*. If two parts from different decompositions in the set, although having a common point which is interior to at least one of them, nevertheless are not coincident overall, then there are a number of different mapping relations which can hold between their boundaries; and the system is said to be *descriptively complex*. On this basis a piece of granite is regarded as descriptively simple, but a *Drosophilia* fruit fly is descriptively complex (Wimsatt 1976).

This account of descriptive complexity provides the necessary basis for formulating another kind of complexity that may be called interactional, since it expresses the extent of the causal interactions of a system, paying attention to those interactions which cross the boundaries designated by different theoretical perspectives. If, for a particular decomposition, the causal interactions within subsystems so identified are all much stronger than those between the subsystems, then we have a case of the "near-decomposability" of Simon (1962). If now we regard these subsystems and the system of which they are a part as respectively identifiable only through the operation of different perspectives, near-decomposability can then be seen as an example of *interactional simplicity*. A system is interactionally simple if none of the subsystems in such a decomposition cross boundaries between its different theoretical decompositions. Correspondingly, a system is *interactionally complex* to the extent that they do so.

Such analyses of the notion of complexity reinforce the intuition that systems of the complexity of the living need more than one perspective to do justice to them, for it is far from clear into what component subsystems living organisms should be analyzed to provide the raw material for the most comprehensive, nonreducible theory—and this is true a fortiori when the component subsystems have evolved together and are not obviously separable (Levins 1970). These analyses also serve to emphasize how difficult it is likely to be to find a quantitative measure of complexity that could embrace such a wide diversity of components and modes of organization. However, attempts have been made to define complexity more precisely and they must be examined.

Wicken (1979) refers to a formalism in information theory whereby a physical system is regarded as a sequence of digits requiring information for its specification, and the complexity of such a sequence is defined as the information content of the briefest algorithm by which the sequence could be unambiguously generated. In this context, a random sequence is one that has to be specified digit by digit, since it exhibits no patterns of regularity expressible algorithmically; and a more ordered sequence is one that can be generated by an algorithm of smaller information content than that required for a random one of the same length—so order and randomness are therefore relative concepts. The complexity of such a physical system, so defined, depends on size and heterogeneity but, more importantly, on its aperiodicity, its lack of regular patterns determined algorithmically. As these features increase in a physical system (i.e., in the sequence), so does the information content of the algorithm needed to specify its structure. (Wicken stresses that it is the aperiodicity which is crucial for allowing a chemical system to evolve.)

P. T. Saunders and M. W. Ho (1976) resort to automaton theory (von Neumann 1966) to define complexity as the number of components a system contains, or rather, for biological systems, as the number of different *types* of components. Increase in such complexity, they claim, is comparatively easy to observe and so provides a practicable partial ordering of species—with the hope that species might be totally ordered in terms of such complexity by utilizing the ranking of organisms that is afforded by knowledge of the minimum DNA content per haploid genome (for this minimum DNA content is a measure of the expressed genetic material which itself must be correlated with the complexity of the phenotype). Saunders and Ho regard complexity, so defined, to be a more fundamental parameter of evolution than organization, which they regard as less easy to define, increases in it arising secondarily because the more complex a system is, the more organization it needs to survive. They see complexity, as they have defined it, as an internal property of a system and assert that it is in the nature of the changes we call evolutionary that such complexity should tend to increase and that this (and not their fitness) is the significantly increasing property of living systems as such. But why, they ask, could it not be said that it is in the nature of complex systems that they should evolve in time with an increase in complexity? Consider, they suggest, a system which is at or near a local peak of fitness, and so has achieved a locally optimal organization. The random *removal* of a component from such a system must tend to make it less fit than before, since previously its organization was optimal in this respect. However, the random *addition* of a component, while it may lead to a decrease in fitness, also allows for the possibility of a subsequent increase in fitness. Furthermore, if a living system is *not* near a local peak of fitness, then there is an additional tendency for complexity to increase because suitable adaptations are more likely to be forthcoming from a larger set of components than from a smaller one (recall their definition of complexity). So in both situations, near or not near to a local fitness peak, the quantity that will be increasing in evolution is, according to Saunders and Ho, complexity, defined in relation to the number of different types of components present in the system. Linking this emphasis of Saunders and Ho on increase in complexity, as the essentially increasing parameter in evolution, with the analysis of Wicken, that the drive towards an increase in complexity at the molecular level is entirely consistent with the second law of thermodynamics, encourages the hope that thermodynamics may in fact be relatable to evolutionary "progress." That will be the concern of the next major section, but we must first consider the somewhat obscure notion of organization in living systems.

Organization. "Organization" in living organisms is widely regarded as of fundamental significance when it is (as we saw above in the section on "The Basic Features of Thermodynamics") distinguished from the order to which entropy is negatively related. For it is clear that, over and beyond complexity described and defined according to the procedures outlined in the previous section, what is distinctive of a biological organization is its ability to perform numerous functions. However, although functions can be readily described and even classified (cf., Miller 1978), they are not readily quantified. So the concept of "functionality" cannot in any obvious way provide a quantitative parameter for the process of evolution. Organized systems have to be distinguished from ordered systems, as we have already seen, since the latter can be generated according to simple algorithms (and so in any case lack complexity [Wicken 1979]) whereas organized systems have to be assembled from diverse components that are linked together in specific ways. Such a blueprint has its own specification and presumably its own "information content." So "organization is functional complexity and carries functional information" (Wicken 1979, 353). This nonrandomness comes about by natural selection because, according to Saunders and Ho (1976), "only systems which are organized can evolve, for organization prevents the loss of components and yet allows increase in complexity through the integration of new ones."

In spite of the obvious difficulty in quantifying a concept as subtle as that of organization, a number of authors have attempted to do so. Denbigh (1975) has extended the definition of complexity coming from automaton theory, a definition that was cast in terms of the number of different types of components in a biological system (see "Complexity" above), by including also the connections between components. He has proposed (Denbigh 1975, 1981) the concept of *inte-*

grality (φ) as a measure of organization and so of complexity. If c = the number of connections which facilitate the functions of the whole, n = the number of different *kinds* of parts, and x = other variables, then

$$\varphi = cn\ \mathrm{f}(x),$$

where $\mathrm{f}(x)$ is a weighting factor taking account of the relative importance of the various connections to the actual existence of the organized system. Clearly, integrality increases with increasing complexity as when, for example, an egg develops into a chick—unlike "information content" which must be remaining constant during this process. Thus integrality can increase in a closed system and is not conserved. It is not identical with information nor is it related to the entropy, for the degree of connectedness is not a conserved quantity and it can change at constant entropy in a sufficiently idealized system in which switches, valves, membranes, and so forth operate reversibly or at least with only small adventitious changes in entropy.

One of the difficulties in applying this interesting suggestion comes at once in the designation of "parts" in order to give a value to n, for there are many different levels in a biological organism that might be chosen as the reference level for distinguishing them (the familiar sequence of molecule, organelle, cell, organ, organism, population of organisms, etc.). Although most biochemists and molecular biologists would have a predilection for choosing the molecular level, there is really no fundamental level of reality that has an obvious priority as a reference, especially if no such ultimately basic level exists (Denbigh 1981, 132-34).

So the integrality of an individual biological organism will always be relative to a given level of analysis, but, even so, it seems clear that φ will rise steadily during the development of an individual organism from the zygote, will reach a plateau value during maturity, and will decline to zero shortly after death. The total of integrality over the earth's ecosystem has increased since life began (Denbigh 1981, 151) but may well be decreasing on other planets. Unfortunately this stimulating suggestion of Denbigh does not seem to have been taken up much by other authors; it does at least point to the significant features of organization without being entangled in the massive theoretical structures of thermodynamics or of information theory, which were devised for other purposes.

Another approach is that of H. Atlan (1974; 1981) who, recognizing that information content as such provides a very poor definition of organization, has developed the thesis that the kinetics of the *change* of information content with time, under the accumulated effects of noise from the environment, can do so. He argues (Atlan 1981) that there have been two major and contradictory trends in defining organization. On the one hand, organization is seen as redundancy, based on constraint between parts, regularity, or repetitive order (the 100% orderliness of the crystal, with zero entropy, $S = k \ln 1 = 0$, is regarded as optimum organization from this perspective). On the other hand, under the influence of information theory, organization is regarded as variety based on nonrepetitive order which is measured by an information content, that is, a degree of unexpectedness related to variety and inhomogeneity. So, Atlan affirms (1974), any formal quantitative definition of organization should involve a kind of optimization process such that any organization would correspond to a compromise between maximum information content (and so maximum variety) and maximum redundancy. He illustrates this compromise by instancing a cultural system contained in a library (Atlan 1981). The culture exists as intermediate between, first, complete independence (no constraints or relations) between the books and, second, mere repetition (maximum redundancy). The latter would reduce the culture to the content of only one book; the former would not be compatible with what we mean by a cultural system, there being no cross-quotations, allusions, references, and so on, between the books.

Atlan summarizes his definition of organization as follows: first, the process of organization of any system is described by the variation of information content with time, and this variation is a combination of the decrease in its maximum information content (computed by assuming complete independence of the parts) with the change in the redundancy which measures the simplicity and order that comes from physically or deductively repetitive order; second, the kind or state of organization of a system is defined by the initial value of this maximum information content, the initial redundancy and a factor related to the overall resistance of the system to noise.

So several parameters are involved in comparing the degrees of organization of different systems, or the same system at different times, and such comparisons would be best expressed vectorially in an appropriate space. Different constraints on these parameters lead to various kinds of organization. Thus a system is self-organizing if it is redundant enough and functions so that its redundancy decreases in time with accumulation of errrors and/or noise—and yet still functions so that its information content increases. Self-organization appears, then, as a continuous disorganization constantly followed by a reorganization with more complexity and less redundancy. What is characteristic of living systems is the existence of different parameters allowing the initial phase of increase of complexity to be more extended and distinguishable than in other physical systems which have a minimum redundancy and in which such an initial phase could exist in principle. The principles of organization are: that provided its initial redundancy and functional reliability are large enough to allow for an observable period of self-organization, a system can react to random environmental stresses by an increase in complexity and variety, so that it appears to adapt itself to its environment during this phase.

This development by Atlan of a theory of self-organization as "complexity from noise" is a natural extension of the "order from noise" principle of H. von Foester (1960) and is conceptually very close to the "order through fluctuations" which lies at the center of the thermodynamic interpretation of living organisms by the Brussels school (see the next section). Furthermore, the idea of organization as a kind of optimization process of organization, involving a compromise between maximum information content (i.e., variety) and maximum redundancy, was based on an analysis of differences in the position from which observations were made (transmission of information within a system, as the functioning of the system in itself, viewed from within, versus the view of the system seen as a whole by an external observer). The observational level discriminated by the external observer is then very critical for what is regarded as lacking in the information that an observer has of the system in question. So this informational theory of self-organization is closely tied in with the levels of hierarchical organization viewed by the observer—and so with the whole concept of the meaning of information in hierarchical self-organized systems. Atlan has summarized his conclusions in this regard as follows: "What appears to the observer as an organizational noise acting in channels between different hierarchical levels, is in fact, for the system itself, the meaning of the information transmitted in these channels" (Atlan 1978, 177).

Perhaps these ideas of Denbigh and Atlan may eventually provide, when developed and assimilated, that definition and quantified parameter of organization which is so much needed. For although complexity may be quantifiable, according to Saunders and Ho who therefore stress its usefulness as a fundamental index of evolution, it is clear that organization is also of fundamental importance. For only systems which are organized can evolve by the natural selective action of the environment and, in doing so, such aperiodically complex systems become functionally organized systems with functional diversity and communicating and expressing functional information. Generation of molecular complexity is a prerequisite for the natural selection effected by the environment and this selective process acts on the differential stability and self-replicative powers of populations of information-carrying molecules, as Eigen and his colleagues have superbly elaborated (Eigen 1971a; 1971b; Eigen and Schuster 1979; Eigen and Winkler 1981; Kuppers 1983).

Note that in these accounts of biological evolution it is no longer simply the continuous tendency towards increased fitness that impels the development in evolution to more and more complex living systems, but, rather, the nature of the process itself is such that both increase in complexity and, concomitantly though not identically, increase in organization are inherent features of the process itself. If this is so, it might be possible to link such increases with thermodynamic interpretations of natural processes, for, as we have already seen, the laws of thermodynamics provide the basis for increase in molecular complexity with time.

THERMODYNAMICS AND THE EVOLUTION OF BIOLOGICAL COMPLEXITY AND ORGANIZATION

Increase in complexity and organization. The biological complexity we actually observe now in the natural world is the product of a long evolutionary history, and different levels in the hierarchy of biological complexity have appeared at successive stages in the history of the earth, as illustrated by table 1. This table emphasizes the truism that today's biological structures are the result of a long process of development from earlier forms, a fact which is disregarded in the kind of calculations that try to estimate, say, the chance of a molecule of a typical protein being formed de novo from its constituent atoms, or even amino acids. Such calculations (a fortiori if complete organisms are considered) usually result, as we saw, in the conclusion that this probability is so low that the earth has not existed long enough for such a complex assembly to appear by the random motion of atoms and molecules—whether this period be that of the total 4-5 × 10^9 years of the earth's life, or the 1.1 × 10^9 years between the formation of the earth (4.6 × 10^9 years ago) and the oldest known rocks (3.5 × 10^9 years ago) containing the remains of living cells (blue-green algae) found in rocks at Warrawoona, Australia. The fallacy of such calculations lies in their ignoring the actual processes whereby complex self-reproducing (initially molecular and macromolecular) systems might self-organize themselves entirely consistently with currently known thermodynamics and chemical kinetics (Peacocke 1983); in ignoring the role of selection of organizations of macromolecules that have favored reproduction rates and, once established, irreversibly channel the evolutionary process in one particular direction (Eigen 1971a; 1971b); and in ignoring the fundamental analyses of the architecture and evolution of complexity made by many authors (see Whyte, Wilson, and Wilson

1969; Weiss 1971; Pattee 1973; Peacocke 1978), in particular Simon (1962).

TABLE 1

THE MAJOR LEVELS OF ORGANIZATION IN ORGANIC EVOLUTION

Level	Examples	Years ago when first appeared
8. Dominance of tool using and conscious planning	Man	50,000
7. Homoiothermic metabolism (warm blood)	Mammals, Birds	150,000,000
6. Organized central nervous system, well-developed sense organs, limbs	Arthropods, Vertebrates	600,000,000 450,000,000
5. Differentiated systems of organs and tissues	Coelenterates, Flatworms, Higher Plants	1,000,000,000 400,000,000
4. Multicellular organisms with some cellular differentiation	Sponges, Algae, Fungi	2,000,000,000
3. Division of labor between nucleus	Flagellates, Other Protozoa (Eukaryotes)	??????
2. Surrounding cell membrane with selective permeability and active transport of metabolites	Bacteria, Blue-Green Algae (Prokaryotes)	3,000,000,000?
1. Earliest self-reproducing organic systems	Free living Viroids (none still living)	??????

(From: Stebbins 1969, 30)

Simon's story of the two watchmakers, Hora and Tempus, illustrates the evolutionary advantages of the modularization that can occur in the assembly of a hierarchy and is worth quoting in full.

> There once were two watchmakers, named Hora and Tempus, who manufactured very fine watches. Both of them were highly regarded, and the phones in their shops rang frequently—new customers were constantly calling them. However, Hora prospered while Tempus became poorer and poorer and finally lost his shop. What was the reason? The watches the men made consisted of about one thousand parts each. Tempus had so constructed his that if he had one partly assembled and had to put it down—to answer the phone say—it immediately fell to pieces and had to be reassembled from the elements. The better the customers liked his watches, the more they phoned him the more difficult it became for him to find enough uninterrupted time to finish a watch. The watches that Hora made were no less complex than those of Tempus. But he had designed them so that he could put together sub-assemblies of about ten

> elements each. Ten of these sub-assemblies, again, could be put together into a larger sub-assembly; and a system of ten of the latter sub-assemblies constituted the whole watch. Hence, when Hora had to put down a partly assembled watch in order to answer the phone, he lost only a small part of his work, and he assembled his watches in only a fraction of the man-hours it took Tempus (Simon 1962, 470).

Simon goes on to make a more quantitative analysis of the relative difficulty of the tasks of Hora and Tempus. If there is one chance in a hundred that either watchmaker would be interrupted while adding one part to an assembly, then a straightforward calculation shows that it would take Tempus, on the average, about four thousand times as long to assemble a watch as Hora! Although, Simon points out, the numerical estimate cannot be taken too seriously (and indeed it can be shown to be too low), the lesson for biological evolution is quite clear. The time required for the evolution of a complex form from simple elements depends critically on the number and distribution of potential, intermediate, stable forms—in particular if there exists a hierarchy of potentially stable "subassemblies."

A more detailed argument shows that in a hierarchy of potential stable subassemblies the time required for a system containing 10^{25} atoms to evolve from one containing 10^{23} atoms is the same as that for a 1000-atom system to evolve from a 10-atom one. Or to put it more broadly and only illustratively, it might well be that the time of evolution of multicellular organisms from single cells is of the same order of magnitude as the time required for the evolution of single-celled organisms from macromolecules (Simon 1962). Indeed, some such principle must lie behind the strong impression that evolution develops exponentially and that only a logarithmic time scale can spread out its many stages in any evenly spaced manner.

Simon showed that complex systems will evolve from simple systems much more rapidly if there are stable intermediate forms than if there are not, and that the resulting complex forms will then be hierarchic in organization. The requirement for stability of an atomic or molecular structure reduces to the requirement that the free energy of the structure be less by virtue of its structure than that of its component atoms or molecules. The complex structures that emerge in the evolution of the first living forms, and of subsequent forms, may be presumed to have a stability of this kind, although, since living systems are open, the stability attributed to them must not be identified directly with the net free energy of formation of their structures. The point that is essential to make here, in relation to the possibility of formation of complex forms, is that natural selection speeds up the establishment of each new stratum of stability in the succession of forms of life. Each stratification of stability is only a temporary resting place before random mutation and natural selection open up further new possibilities and so new levels of (temporary) stability—rather as if the free energy profile were a switchback with any given form stable only to the immediate environment of the controlling parameters and always with a finite chance of mounting the next barrier to settle (again temporarily) into a new minimum.

J. Bronowski (1970) has also pointed out that this "stratified stability," which is so fundamental in living systems, gives evolution a consistent direction in time towards increased complexity. He used the metaphor of evolutionary time as a "barbed arrow," because random change will tend in the direction of increasing complexity, this being the only degree of freedom for change—and, as we saw above, Saunders and Ho (1976) have also produced a neo-Darwinian argument along similar lines for the inevitability of increases in complexity in evolution.

Thermodynamic interpretations of evolution. Living systems are open in the thermodynamic sense, that is, they exchange matter and energy with their environment. It is possible for such open systems to evolve towards a steady state in which the total entropy (and indeed all other macroscopic parameters) of the system remains unchanged, since it is then constituted by two balancing and exactly cancelling components: an increase in entropy in any time interval resulting from the irreversible processes occuring in the system and a decrease in entropy due to loss of heat to the surroundings (which thereby undergo an increase in entropy). Internal entropy production (d_iS/dt), due to the natural processes occuring in the steady state of an open system, is a characteristic feature of such a system. It was an early discovery of irreversible thermodynamics (Prigogine 1947) that, when driving forces have a linear relation to resulting fluxes (and when certain other, not unduly restrictive conditions apply), the entropy production can be shown to be constant and at a minimum with respect to its values as it approaches the steady state (e.g., see Peacocke 1983, 35-40). This requirement for linearity restricts the applicability of the above principle to real systems not far removed from equilibrium, for only then can forces and fluxes be related linearly in all instances.

H. J. Hamilton (1977) assumes that open systems that involve nonlinear irreversible processes (which means in practice most real systems, including living ones) also obey this principle of the entropy production being minimal in the steady state.[3] He then goes on to show that, on this basis, the probability that a particular kind of complex will be formed by the addition of one or another kind of element to an existing large complex (or the frequency of occurrence of such a complex in a large population of systems) is greater the lower the value of specific entropy production of the new complex.[4] He calls this thermodynamic criterion for the coming into existence of a new complex "the principle of thermodynamic selection" and then applies it to the spontaneous creation and hierarchical evolution of all ordered structures—in particular to the successively and increasingly complex living systems of biological evolution—so that "the principle of natural selection thus may be formulated in terms of fundamental thermodynamic laws and will be seen to be a special application of the principle of thermodynamic selection" (Hamilton 1977, 316). He goes even further, affirming that "the principle of natural selection, thus formulated, has the character of a fundamental physical law. Self-reproducing systems with suitably open hereditary programs may combine to form stable social systems, which may grow and reproduce as a unit. In this way self-reproducing systems of increasing hierarchical order, size, and organizational complexity may evolve through processes of thermodynamic (natural) selection" (Hamilton 1977, 289).

These ideas of Hamilton constitute a thoroughgoing attempt to interpret the form (and even the behavior) of living systems and the processes by which they have evolved in terms of thermodynamics—and so in terms of fundamental physical laws. Its principal weakness is that it rests on an unproven and, so far, not adequately empirically substantiated premise, namely, that the steady state(s) of nonlinear open (and closed) systems are characterized by having a minimum entropy production. Indeed, the time variation of the entropy production has no special properties for such nonlinear systems and only part of the entropy production (that due to changes in the forces operative) may be used as a criterion of evolution according to the Brussels school (Prigogine, Nicolis, and Babloyantz 1972; see the account given by Peacocke 1983, 42-50). So the status of Hamilton's principle of thermodynamic selection remains problematic and, for the moment, does not provide a secure enough basis for a uniquely thermodynamic interpretation of biological evolution. Broadly, it seems thermodynamically feasible to associate a reduction in entropy production with a decrease in the dissipation of energy and so with maximizing the utilization of energy, which must help survival of a living system. However the argument is not yet really rigorous enough, in my opinion, to affirm confidently that there is such a principle of thermodynamic selection with respect to minimal entropy production that is operative in biological evolution and uniquely determinative of its course.

That the biosphere is one of the temporary "residences" of (free) energy in its flux from the sun via the earth's surface on its way again to outer space has already been stressed in the above section on "Evolution and Thermodynamics—the Problem?" Over the time scale of existence of most biological organisms (even that of the species rather than of the individual organism), this flux corresponds to a steady state with overall inward flow balanced by flow outward. However, just as in a stream passing down a rocky gorge, flows can vary within the overall movement while the general movement is nevertheless in one direction, so too it is pertinent to relate these energy fluxes to the general direction of biological evolution. Thus, in his now classic work on *Elements of Physical Biology*, A. J. Lotka wrote as follows in 1924:

> *Collective Effect of Individual Struggle for Energy Capture.* Our reflections so far have been directed to the selfish efforts of each organism and species to divert to itself as much as possible of the stream of available energy. But... we shall be led to enquire: What must be the effect, upon the world-as-a-whole, of the general scrimmage for available energy?... If we had only the animal kingdom to consider we should in the first instance be disposed to conclude that the cosmic effect of the scrimmage for available energy would be to increase the total energy flux, the rate of degradation of the energy received from the sun. But plants work in the opposite direction.... There are thus two opposing tendencies in operation, and it is difficult to see how any general principle can be applied to determine just where the balance will be struck.
>
> *The Law of Evolution Adumbrated as a Law of Maximum Energy Flux.* This at least seems probable, that so long as there is an abundant surplus of available energy running "to waste" over the sides of the mill wheel, so to speak, so long will a marked advantage be gained by any species that may develop talents to utilize this "lost portion of the stream." Such a species will therefore, other things equal, tend to grow in extent (numbers) and this growth will further increase the flux of energy through the system.... Every indication is that man will learn to utilize some of the sunlight that now goes to waste. The general effect will be to increase the rate of energy flux through the system of organic nature, with a parallel increase in the total mass of the great world transformer, of its rate of circulation, or both.
>
> One is tempted to see in this one of those maximum laws which are so commonly found to be apt expressions of the course of nature. But historical recollections here bid us to exercise caution; a prematurely enunciated maximum principle is liable to share the fate of Thomsen and Berthelot's chemical "principle of maximum work" (Lotka [1924] 1956, 356-58).

The note of caution at the end is certainly worth taking to heart for it is not at all clear how this flux and its associated entropy increase, that is, "randomization" of energy with time, is to be related to biological development or evolution. In the section on "Evolution and Thermodynamics—the Problem?" we saw that order, in the strictly thermodynamic sense as related to the number of complexions in the system (W), *can* be generated in purely physical systems while operating strictly under the mandate of the second law, that is, with entropy increasing in a natural, irreversible process. Moreover, we saw too that such order can arise spontaneously in a system (technically a closed one) such as a tube containing a gas in contact with a source of heat at one end but not at the other, through which thermal energy is flowing. The structure so formed—in this instance merely a gradient of increasing molecular concentration in the same direction as the energy flow—serves to reduce the *rate* at which the energy flows, and so decreases the rate of energy dissipation and the rate of production of entropy, to levels which both H. J. Morowitz (1968) and Hamilton (1977), in describing this system, affirm must be minimal. Certainly there is a reduction and therefore an increase in the "residence time" of the energy in the system itself. Morowitz (1968; 1974) argued that in biological evolution these thermodynamic effects will favor the emergence of new species that have an increased residence time before it is passed out as heat to the surroundings. Of course, the total overall flow of energy from the sun via the earth to outer space is not, in the long run, affected by living organisms on the earth's surface, but (as in Lotka's mill wheel analogy, or as for eddies in a stream) this does not prevent particular living organisms from existing in their own adaptive niches by having an increased efficiency of energy utilization, a decreased dissipation of energy and entropy production, and so a longer residence time for the energy in the organism.

Here a difficulty arises. Is one referring in this to the individual organism or to a population of organisms? For there are grounds for thinking (see, e.g., Wicken 1980) that, as evolutionary expansion into new adaptive zones (or individual biological development) proceeds, the total dissipation of the evolving ecosystem or developing organism often increases rather than decreases. It becomes crucial to decide to which unit one is referring: individual organisms or populations, in the context of evolution; or the individual embryo or the whole organism, in the context of development? Wicken affirms that "if the principle of decreasing dissipation applies in biological evolution, it can only be with respect to the whole, quasi-closed ecosystems, to interacting webs of populations, rather than to individual species" (Wicken 1980, 14-15).

Many other factors are involved in success in competition, as the sociobiologists would be quick to point out, but Wicken nevertheless regards it as safe to affirm that, considered as wholes, the evolution of ecosystems is bound by the general thermodynamic principle of decreasing energy dissipation. More particularly, when there is a constant overall energy flux in a particular ecosystem, he affirms that this principle predicts that further increases in the total mass of organisms can occur only through reductions in the mean specific (i.e., per unit) dissipation of its energy-transforming components (presumably the individual organisms).

As with Hamilton's extension of the principle of minimum entropy production from linear to nonlinear open and closed systems, this is all plausible and, indeed, probable. The bother is that it lacks a coerciveness that can come only from experimental studies on the energy fluxes and rates of entropy production in actual biological systems, whether a developing embryo or organ in relation to an organism, or an organism in relation to a population of organisms, or the latter in relation to its whole ecosystem. Until these are forthcoming we are perforce in the realm of reasonable conjecture and not of proven and tested application of thermodynamic principles. However, what does emerge from these and other proposals is the broad consistency and coherence with thermodynamics of the possibility and direction of biological evolution. In particular, in the light of the way in which the energy-randomizing character of irreversible processes—the basis of the second law—drives transformations in the actual existing world of atoms and molecules to structures of greater complexity (section above on "Evolution and Thermodynamics—the Problem?") a thermodynamic interpretation renders more intelligible the tendency for there to be an increase during evolution both in complexity and in any functional organization that enhances efficiency of energy utilization in individual organisms and minimizes energy dissipation (entropy production) in whole ecosystems.

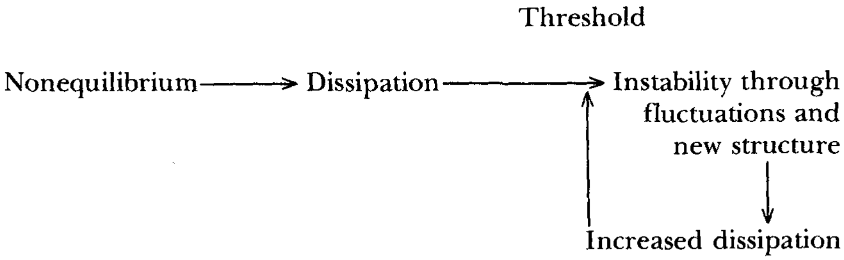
The origin of living systems from the nonliving and dissipative structures. One of the particular achievements of thermodynamic theory in the last few decades has been its provision of a basis for understanding the spontaneous coming into existence, as distinct from the maintenance, of organized structures (which may be as much kinetically as topologically organized) in open (and closed) systems far from equilibrium when flux-force relationships are nonlinear. This analysis by the Brussels school, under the leadership of Ilya Prigogine, has significance especially for understanding the emergence of functionally and structurally organized living matter from nonliving, that is, nonself-copying, matter (for references see Peacocke 1983, 17-72). They have been able to show how, on a strictly thermodynamic basis, new organized forms of systems can (but not necessarily will) come into existence and be stable, if matter and energy are flowing through to maintain them. These new ordered forms are called "dissipative structures" and are radically different from the "equilibrium structures" studied in classical thermodynamics, the order of which is attained only at low enough temperatures in accordance with Boltzmann's ordering principle (as described above and coupled with $\exp(-E/k_B T)$ being proportional to the probability of occupation of a state of energy E at temperature T). In this nonlinear range, nonequilibrium can indeed be the source of an order that would not be predictable by the application of Boltzmann's principle. In such states there can occur, under the right conditions, fluctuations that are no longer damped and that are amplified so that the system changes its whole structure to a *new* ordered state, in which it can again become steady and imbibe energy and matter from the outside and maintain its newly structured form. This instability of dissipative structures has been studied by these workers who have set out more precisely the thermodynamic conditions for a dissipative structure to move from one state to a new state which is more ordered than previously, that is, for order through fluctuations to occur.

It turns out that these conditions are not so restrictive that no system can every possibly obey them. Indeed a very large number of systems, such as those of the first living forms of matter which must have involved complex networks of chemical reactions, are very likely to do so, since they are nonlinear in the relationship between the forces and fluxes involved. The ordered configurations that emerge beyond such an instability of the thermodynamic branch of nonlinear systems were called dissipative structures, because they are created and maintained by the entropy-producing "dissipative" processes occurring inside the system through which, being open, there is a continuous flux of matter and energy.

Model physical systems undergoing such transitions are now well known, for example, the famous Bénard phenomenon where a hexagonal organization at right angles to the vertical heat flow is observed, at a certain critical point, in a column of liquid heated from below—and others cited by H. Haken (1978) who, because the awareness of them has now become so widespread and because they share common features in the "bifurcation" of the solutions of the differential equations controlling these phenomena, has invented a new name for the study of such systems, namely "synergetics."

Even more pertinent to biological systems is the observation of order-through-fluctuations in chemical systems. Chemical networks can be of a very high degree of complexity through incorporating one or more autocatalytic steps, and they are often nonlinear (in the sense above) when not close to equilibrium. Then various kinds of oscillating reactions and other features can occur. One of the most striking of these is the so-called Belousov-Zhabotinsky reaction, the oxidation of malonic acid by bromate in the presence of cerium ions in solution (Tyson 1976). With the right combination of solution conditions and at constant temperature, the original homogeneous reaction mixture changes into a series of pulsing waves of concentration of cerium ions, moving up and down the tube, until eventually a steady state is reached in which there are static, banded layers of alternating high and low concentrations of ceric ions. From an originally homogeneous system, a highly ordered structure has appeared through the fluctuations that are possible in a nonlinear system far removed from equilibrium. What has happened is that fluctuations in such a system have been amplified and, consistently with the laws of chemical kinetics, a new structure has appeared that is ordered, at first in time and then finally in space, representative of an alliance of chance and law. Under the conditions of this reaction the structural formation has a probability of unity, provided that the initial fluctuation arises from within the system. The causal chain leading to this fluctuation, although it cannot be discerned by ourselves, must itself be the result of law-like processes occurring at the micro level. Because of the discovery of these dissipative systems and of the possibility of order-through-fluctuations, it is now possible, on the basis of these physico-chemical considerations, to regard as highly probable the emergence from nonliving matter of those ordered and articulated molecular structures that are living. Instead of them having only an inconceivably small chance of emerging in the "primeval soup" on the surface of the earth before life appeared, we now see that ordered dissipative structures of some kind will appear in due course.

One has to presume that before life had evolved there existed in this prebiotic stage a system containing replicating macromolecules that could both maintain itself by means of some simple copying mechanism and have a potentiality of change incorporated into its very structure and function so as to facilitate its multistage evolution to more complex forms more efficient in survival and reproduction. Some of the kinetic and stochastic problems associated with such prebiotic systems have been very fully investigated by Eigen and his colleagues at Göttingen, Germany (Eigen 1971a; 1971b; Eigen and Schuster 1979). In the present context we raise the question asked by Prigogine and his colleagues from a more thermodynamic perspective which may be put thus: How can each step in an evolutionary process in which each stage leads to more orderly, or at least more complex, configurations contain within itself the potentiality to change by other, later transitions to yet more ordered, complex configurations? Each transition to be part of a *continuous*, multistage evolution cannot become a dead end, that is, it must contain within itself the possibility of yet further changes—otherwise the system is simply eliminated in the competition for limited "food" reserves (of simpler monomers, in this case). What is needed is for change to occur in such a nonlinear open system in a way that increases its nonlinearity and distance from equilibrium and thereby both ensures and enhances the possibility of further change. This could come about by the change, however brought about, being of such a kind that it increased the interactions between the system and its external environment, such interactions being one of the causes of nonlinearity. If this were to happen, this increase of interaction would be reflected in an increase in the entropy production per unit mass, that is, there would be an increase in the dissipation in the system as an immediate consequence of the transition. This increased dissipation would then, temporarily at least, characterize a system which had the potentialities of undergoing further instabilities when appropriate thresholds were passed, and so of forming new structures, with again increased dissipation, and so on. A kind of feedback in evolution of such nonlinear systems has therefore been postulated by the Brussels group (Prigogine, Nicolis, and Babloyantz 1972) that may be depicted as:



Once this instability has been initiated, it is proposed, the system can increase its specific entropy production, which they take as a suitable index of the level of dissipation in a system.[5] Each instability would be followed by a higher level of energy dissipation, which would mean some of the irreversible processes in the system would be working more intensely, would therefore depart further from equilibrium, and so would enhance the probability that there should occur those kinds of fluctuations that would again render the processes unstable. Members of the Brussels group have been able to show that quite large classes of systems in which biological macromolecules are being synthesized can display this "evolutionary feedback," principally because the transitions that increase the relative numbers of copies of such macromolecules must have certain autocatalytic properties.

Further calculations suggested to them that those systems that display an *increase* in dissipation as manifest in the specific entropy production do so only transiently, after the initial threshold fluctuation. For once it is in the new regime that can display this initial enhancement of dissipation, it seems, from the available thermal data, that the system adjusts itself to the constraints and that the dissipation then tends to *decrease* to a new level characteristic of the new nonlinear steady state (now further than before from equilibrium). As Prigogine et al. say: "one is tempted to argue that only after synthesis of the key substances necessary for its survival (which implies an increase in dissipation) does an organism tend to adjust its entropy production to a low value compatible with the external constraints" (Prigogine, Nicolis, and Babloyantz 1972, box inset).

As already mentioned, for a nonlinear system to evolve it must undergo changes which are of such a kind that they still, after the change, possess the potentiality of further change. However, this state of affairs could not continue indefinitely, and indeed there was evidence that eventually the entropy production could decrease to a new value characteristic of the new (dissipative) structure. The creating of structure leads to an increase in entropy production whereas maintenance of the structure once formed, it is suggested, could obey the theorem of minimum entropy production. On this interpretation, entropy production would pass through a series of decreasing minima, transitions between which occur via a temporarily enhanced increase before falling to the next lower minimum (Prigogine, Nicolis, and Babloyantz 1972).

The idea of a succession of temporarily stabilized states as being a useful perspective on evolution was also proposed by Bronowski (1970) when he pointed out that stratified stability was the principal feature of the evolutionary sequence, both inorganic and organic. Each more complex form represents a new stratum of stability which has a finite chance of forming under the conditions appropriate to it. His picture of evolution is that, once formed, each stratum of complexity has a stability which allows the possibility for the next stratum to appear by providing the structures (atomic, molecular, organic, or whatever) which form the constituent building blocks of the next level. "Because stability is stratified, evolution is open and necessarily creates more and more complex forms. . . . So long as there remains a potential of stability which has not become actual, there is no other way for chance to go. It is as if nature were shuffling a sticky pack of cards, and it is not surprising they hold together in longer and longer runs" (Bronowski 1970, 32). Bronowski speaks here of chance (which is related to entropy), but the strata to which he refers are levels of *energy* minima, successive ones higher in energy than the preceding, and each reached over an energy barrier—rather like ascending and descending a succession of cols into a series of valleys in a mountain range, the level of each valley bottom being higher than its predecessor.

This interpretation is given a more sophisticated thermodynamic content in the treatment of the Brussels school. In their exposition, too, it is not instability but a succession of instabilities of dissipative systems, now appearing under the aegis of thermodynamic laws, that bridges the gap between the nonliving and the living. This succession of instabilities can be a process of self-organization, and so of evolution, provided there are fulfilled certain conditions that emerge clearly from the foregoing thermodynamic considerations. They are that a process of self-organization can occur in a system if, first, the system is *open* to the flux of matter and energy, second, the system is not at equilibrium and preferably *far from equilibrium*, and, third, the system is *nonlinear* in its flux-force relationships, that is, there is strong coupling between its processes. These simple requirements underlie the ideas developed above, notably by the Brussels school, and are certainly satisfied by all biological systems and organisms. Therefore, the following "theorem," formulated by G. Nicolis, is applicable to them and serves to summarize the whole analysis: "Consider a single phase system satisfying the above three prerequisites [conditions], whose entropy can be defined in terms of macroscopic quantities. Under these conditions, steady states belonging to a finite neighborhood of the state of thermodynamic equilibrium are *asymptotically stable.* Beyond a *critical distance* from equilibrium they *may* become unstable" (Nicolis 1974).

The evolution to order through an instability induced by fluctuations, referred to in this last sentence, is only a possible, not a certain, development and in fact requires, along with the subsequent stabilization to a dissipative structure, that some other very stringent conditions be fulfilled.

Thermodynamics and kinetic mechanisms. The existence of these other conditions remind us that, like patriotism, thermodynamics "is not enough." For thermodynamics is always the science of the possible: it can allow, it can forbid, but it cannot prescribe. What actually occurs in any system obeying the conditions described above for it to become (more) self-organizing depends on the ability of the actual molecules and higher structures present, on their spatial and temporal arrangement, and on the numerical parameters specific to these features. In a molecular system this means the patterns generated will depend principally on chemical reaction rate constants and on diffusion constants, controlling movement across space. Similar parameters characteristic of higher order structures will also operate at other levels, for example, in the patterning in predator-prey, herbivore-plant, and host-parasite systems (Lotka [1924] 1956). Ever since the seminal paper of A. M. Turing (1952) on "The Chemical Basis of Morphogenesis," it has become increasingly clear that suitable combinations of rates of chemical reactions and diffusion processes can spontaneously generate patterns in space and time, both permanent and oscillating according to conditions. This separate development of dynamical theory, of kinetics, and of fluctuation theory opens up new vistas of interpretation of pattern formation at many levels of biology, and even in social structures according to the Brussels group (Lepkowski 1979).[6] These interpretations cannot be described here (see Peacocke 1983, 111-213) but, the point is, it is now possible to understand the detailed mechanisms in actual dissipative systems that lead to new ordered (self-organized) forms appearing.

Particularly striking biological examples of such forms are provided by the oscillations in time and the patterning in space of the concentration of intermediates in glycolysis that have been observed by Benno Hess and his colleagues, and by the quite extraordinary ability of individual unicellular slime mould organisms (in particular *Dictyostelium discoideum*) to come together, under conditions of starvation, in organized spiral and annular patterns in a colony that then behaves, temporarily, as an organized whole until new food sources are found (references in Peacocke 1983, 111-213).

So, one may well ask, what *is* to be gained from the application of irreversible thermodynamic concepts and criteria to biological systems? The primary and overriding gain is undoubtedly in the ability of thermodynamics to provide, as it were, an architectonic framework which limits but does not in detail prescribe. One can then build on this framework by using other resources of dynamical theory, of kinetics, of fluctuation theory—and of precise experimental information and new knowledge of modes of control and regulation at all levels in biology. Structural order comes from the existence of constraints, and the macroscopic and phenomenological approach of thermodynamics is uniquely fitted to handle such factors. Thus the thermodynamic analyses we have been descibing can serve to eliminate some putative models of biological situations as being incompatible with macroscopic physical laws, while permitting others, if not actually determining the choice between them. This can be a useful role, since so much of theoretical biology is concerned with formulating and testing mathematical models of the phenomena in question, and thermodynamics can be a help, for example, in restricting the rate laws that might be relevant. Indeed for some areas of theoretical enquiry, the thermodynamic constraints on the building of models are often the most reliable knowledge of the situation available—for example, in any modelling of prebiotic evolution.

So thermodynamics can never work in isolation from other approaches based on the theory of fluctuations, of stability, of stochastic processes, and of nonlinear differential equations. However, it has its own unique insights which serve to link reflection on biological systems with the whole corpus of physico-chemical theory. For the new concepts in irreversible thermodynamics of nonequilibrium as the source of order, of order through fluctuations, of the decisive role of nonequilibrium constraints, and of dissipative structures (spatial, temporal, and both) in open systems broaden and deepen immeasurably our perspective on biological systems and whole organisms and, indeed, have already proved to be a stimulus for the kind of detailed work that is required to give them a "local habitation and a name."

CONCLUSION

At the beginning of this paper I quoted a paragraph of Norbert Wiener in which he seemed to be suggesting that a thermodynamic perspective provoked the feeling that the universe was somehow against the experiment of life and that in nurturing our little enclave of organized existence, as biological and as social systems, we were swimming against the entropic stream that was in fact sweeping all to randomness and "dark night." But the picture that is emerging in more recent thermodynamic analyses of dissipative systems and of living organisms has a different tenor. Certainly the stream as a whole moves in a certain general, overall direction which is that of increasing entropy and increasing disorder, in the specific sense I have defined. However, the movement of the stream *itself* inevitably generates, as it were, very large eddies *within* itself in which, far from there being a decrease in order, there is an increase first in complexity and then in something more subtle—functional organization. Now there could be no eddies without the stream in which they are located. So may it not be legitimate to regard this inbuilt potentiality for living organization that the entropic stream manifests as being its actual point, namely, why it *is* at all? There could be no self-consciousness and human creativity without living organization, and there could be no such living dissipative systems unless the entropic stream followed its general, irreversible course in time. Thus does the apparently decaying, randomizing tendency of the universe provide the necessary and essential matrix (*mot juste*!) for the birth of new forms—new life through death and decay of the old.

NOTES

1. Furthermore, new composite properties, a combination of U and S with P, V and T could be devised, e.g., the "Gibbs free energy," $G = U + PV - TS$, and heat content, $H = U + PV$. So $G = H - TS$ and this is an important criterion of equilibrium at constant temperature and pressure, for then $dG = 0$.

2. See also comments on this in relation to Teilhard's pan-psychism in Peacocke (1979).

3. This also applies to closed systems, in which there is tranference of energy but not of matter, as distinct from isolated systems, in which there is no energy or matter transference. Here, and in what follows, *open* will usually be taken to include *closed* in this technical sense.

4. *Specific* entropy production (s.e.p.) = entropy increase per unit time per unit mass.

5. For a definition of *specific entropy production* see note 4.

6. But the cautionary note sounded by Wicken (1979, 285-300, esp. 299-300) with reference to the transferring of thermodynamic concepts to the social sciences is worth noting. Such a transference certainly looks, in the first instance, like an illegitimate application of principles valid in one domain to another where their application is inappropriate. However cross-fertilization by analogy and metaphor can often prove to be a creative stimulus as long as it is recognized as such—and is not a concealed reductionist ploy.

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