THERMODYNAMICS OF TERRESTRIAL EVOLUTION

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ABSTRACT The causal element of biological evolution and development can be understood in terms of a potential function which is generalized from the variational principles of irreversible thermodynamics. This potential function is approximated by the rate of entropy production in a configuration space which admits of macroscopic excursions by fluctuation and regression as well as microscopic ones. Analogously to Onsager's dissipation function, the potential takes the form of a saddle surface in this configuration space. The path of evolution following from an initial high dissipation state within the fixed constraint provided by the invariant energy flux from the sun tends toward the stable saddle point by a series of spontaneous regressions which lower the entropy production rate and by an alternating series of spontaneous fluctuations which introduce new internal constraints and lead to a higher entropy production rate. The potential thus rationalizes the system's observed tendency toward "chemical imperialism" (high dissipation) while simultaneously accommodating the development of "dynamic efficiency" and complication (low dissipation).

INTRODUCTION

Philosophers and scientists have long sought a scientific basis for the regularities which are observed in the development of matter at the higher organic levels. Herbert Spencer (1900) was so impressed by the laws of evolution as expounded by Charles Darwin that he attempted to extend the application of these empirical laws outward to the dynamics of human relationships as well as inward to the physics and chemistry of inanimate matter.

In the 20th century the success of physico-chemical methodology has given impetus to the search for a general statement which will encompass the apparent progressive trend of terrestrial evolution. The works of Oparin (1953), Blum (1951), Johnson *et al.* (1954), and the modern microbiologists (Edds, 1961; Oncley, 1959) have clearly delineated the thermodynamic and molecular nature of processes and transitions in animate matter.

Microbiology has achieved an outstanding success in elucidating the microscopic building blocks of evolution and their static relationships, but it has had very little that is concrete to say about the regulative and cooperative phenomena[1] which compose the kinetics of biological processes (Bonner, 1960). Indeed, one often detects a hint of anthropocentrism in statements about the attributes of the microbiological units.

Purposiveness in physical systems is best expressed in the form of a potential function, particularly if the detailed mechanical connections are too complicated to allow the calculation of the direct causal chain. In simple systems such functions can often be derived uniquely from the mechanical equations. However, for the macroscopic systems to which we apply thermodynamics, our statements of potential control must in their most general forms be regarded as postulates. This postulational nature does not in any way detract from our faith in the applicability of the method. Our doubt extends only to the correctness of the particular choice of potential and to the degree of accuracy of the predictions based thereupon.

Lotka (1945) has been a strong proponent of this approach and has accordingly sought a variational principle which would be all inclusive of terrestrial kinetic phenomena. Although he did not have at his command the powerful synthetic methods of irreversible thermodynamics, he nonetheless arrived at a viable answer on empirical grounds. We shall have cause to refer to his solution in a later section.

Prigogine and Wiaume (1946) were the first to draw attention to the possible role of the variational principles of irreversible thermodynamics in the solution of this problem. For example, they have tried to rationalize the tendency for a decrease in rate of metabolism per unit volume with increase in size within phyla on the basis of the principle of minimum entropy production. Furthermore, since the regression towards a steady state of minimum entropy production is often accompanied by a decrease in entropy they find a justification for the Lamarckian view that there is a natural tendency in living material towards "complication." Unfortunately, the empirical fact of evolution is that tendencies towards kinetic efficiency and complication are sometimes reversed so that the principle of minimum entropy production as it stands is quite inadequate to the problem at hand. The rejection of Lamarckism by modern evolutionists on empirical and theoretical grounds may explain, in part, their almost complete neglect of this important contribution.

It has been our view for a number of years that the key to the problem does, in fact, lie in such methods of irreversible thermodynamics. Aware of a missing link in the methodology we have chosen to concentrate on a number of steady state inorganic systems in which analogous problems of causation appear. The results of this work appear in the preceding papers of this series (Kirkaldy, 1959, 1960*a*

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[1] We use the term cooperative in the physico-chemical sense as referring to systems with correlated molecular motions. Order-disorder processes and phase transformations are familiar examples of cooperative phenomena. In the absence of a detailed kinetic description or statement of potential control, the course of such reactions appears to be indeterminate.

and *b*, 1964*a* and *b*, hereinafter designated as A, I to IV). These papers treat certain constrained (steady) systems undergoing phase transformation and fluid flow which become unstable at critical values of the adjustable constraint parameters. When such critical parameters are exceeded it can be demonstrated that a perturbation caused by fluctuation will tend to grow and carry the system towards a more stable state.

It is the contention of this contribution that the sum total of the regression and fluctuation phenomena which constitute terrestrial evolution can be mapped onto an appropriate potential surface and that the causal element of evolution is nothing more than the earth's incessant search by regression and fluctuation for the stability point within the extremely complex constraints provided by environment and geomorphology.

THE THERMODYNAMIC FORMALISM

In the previous papers of this series, and particularly in IV, the stability of dissipative systems was discussed in terms of the potential functions of irreversible thermodynamics. In general, the problem of stability can be discussed in two ways. Calculation of the growth and decay of perturbations of a given state is a common technique (Wagner, 1956; Chandrasekhar, 1961; Mullins and Sekerka, 1963, 1964; Glansdorff and Prigogine, 1964). While effective for testing the stability of a given state this method is often incapable of describing the subsequent evolution of the unstable system without added statistical assumptions. The invocation of a potential function can, on the other hand, make an equivalent test of the stability of a steady state and at the same time, can often yield a measure of the average subsequent evolution of the system. The existence of such a potential function in thermodynamics requires that any intermediate state be accessible from a very large number of prior states so that the system "forgets" its antecedents at each stage of development.

Mathematical tractability usually demands that the thermodynamic potential apply to a path which does not depend explicitly on the time. The entropy maximum principle for an isolated system, for example, applies strictly only to a composite system passing through successive states of constrained equilibrium in the approach to final equilibrium; *viz.*, a quasi-equilibrium path (Callen, 1960). In our previous papers we have discussed the approach to a stable *steady* state *via* an analogous constrained or quasi-steady path. This was an extremely important restriction, for Glansdorff and Prigogine (1964) have demonstrated that a potential function which traces a time dependent path will often contain reversible terms (*e.g.*, changes in kinetic or surface energy). Such terms appear in the quasi-steady path only as part of the constraints.

It was the premise of paper IV that a stable steady state of a materially open system can be represented approximately by a saddle point in the configuration surface of entropy production (rate). This state is a minimum with respect to macroscopic regression within the constraints (Prigogine's principle) or with respect to those microscopic fluctuations of the fluxes with fixed forces which are not reflected in a change in the boundary fluxes (Onsager's minimal principle). It is a maximum with respect to microscopic fluctuations in the fluxes with fixed forces which are reflected in a change in boundary fluxes (Onsager's maximal principle). Examination of a particular inorganic system with internal surfaces (constraints) suggested that a free macroscopic regression following release of an internal or external constraint will often lead to a final state which is unstable with respect to those microscopic fluctuations which stabilize in a state of maximum entropy production. This may give rise to oscillating or fluctuating (dendritic) configurations. The situation is indicated schematically in Fig. 1.

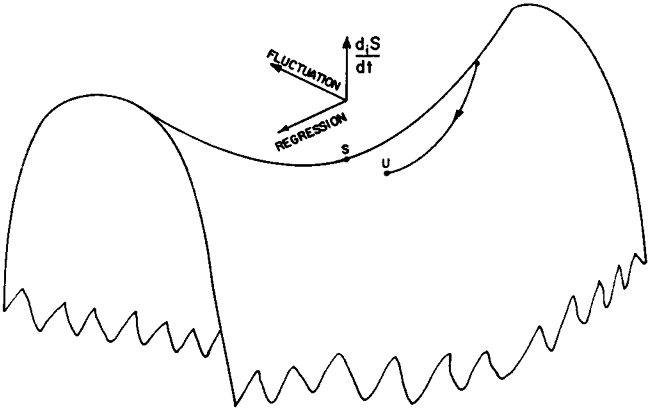

FIGURE 1 Schematic saddle surface of entropy production rate showing a regression path which ends in an unstable minimum.

The question next arises: is there a spontaneous process by which such an unstable system can get closer to the saddle point, and therefore to a more stable configuration? The answer is yes, provided new internal constraints can develop through fluctuation. Indeed, since the release of a constraint leads through regression to a decreased entropy production it follows that an added constraint leads to an increased entropy production rate. For the inorganic systems thus far considered in IV these constraints appear in the form of new surfaces.[2] It is the succes-

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[2] It appears inadvisable at this point to try to define the term "constraint" too precisely. It will suffice to say that current macroscopic experience identifies constraints as fixed values of certain state variables or fluxes at external or internal surfaces. It is characteristic of internal constraints that their release or augmentation must be preceded by a microscopic fluctuation. The internal channels which can be opened by fluctuations are, of course, dependent on the external constraints and the number of such channels generally increases with the intensity or number of external constraints. The introduction of the concept of a "genetic constraint" may require a broadening of this macroscopic concept of a constraint. This is discussed in a later section.

sive nucleation of such surfaces to relieve supersaturation which allows a eutectic to achieve that high dissipation rate configuration which is stable against microscopic fluctuation (IV). We may regard this tendency of the system to maximize the entropy production by nucleation of constraints as the complement of Onsager's microscopic maximal principle.

In full knowledge of Oparin's (1953) warning against the dangers of using inorganic models for biological systems we will present the premise that the regulatory and developmental aspects of biological phenomena can be understood on the basis of the variational principles of irreversible thermodynamics. In view of the difficulty of treating simple inorganic systems quantitatively, we cannot expect to achieve any quantitative relations for biological systems at this point. Nonetheless, we shall find that this formalism will immediately provide a powerful and economic method of classification of the diverse biological phenomena.

THE TERRESTRIAL ENTROPY BALANCE

From the point of view of irreversible thermodynamics the earth may be assumed in good approximation to exist within constant boundary conditions which constrain it from attaining the equilibrium state. The essentially constant source of solar energy in combination with the "hot house" effect of the atmosphere provides a fixed available energy (or entropy) inflow. While the energy (heat) inflow is closely balanced by the energy outflow so that the system remains approximately isothermal, the available energy is degraded within the system so that the entropy outflow exceeds the inflow. This can be expressed quantitatively by the entropy balance

$$\frac{dS}{dt} = \frac{\vec{J}_q}{T_i} - \frac{\vec{J}_q}{T_o} + \frac{d_iS}{dt} \tag{1}$$

where dS/dt is the rate of change of entropy within the system, $\vec{J}_q$ is the heat inflow or outflow, T_i and T_o are effective temperatures of incoming and outgoing radiation, respectively, $(T_i > T_o)$, and d_iS/dt is the rate of entropy production within the system due to irreversible processes. According to Blum (1951), T_i corresponds to a wave length distribution with a maximum at an incoming wave length of 4800 A and T_o to a distribution with a maximum at an outgoing wave length of 10,000 A. Since the constraint on the system is given by

$$\vec{J}_q \quad \text{and} \quad T_i = \text{constant}, \tag{2}$$

change within the systems can be manifested in independent variations of two of the three remaining terms in the balance.

THE COURSE OF GENERAL EVOLUTION

The initial chemical evolution described by Oparin (1953) may be thought of as a regressive process with a corresponding decrease in d_iS/dt. Since the surface temperature need not have changed during this stage dS/dt would be negative with a corresponding accumulation of available energy in the form of higher hydrocarbons. Klein's (1958) model of photosynthetic processes may be regarded as a prototype of those early processes which tended to minimize the rate of entropy production.

In view of the complex internal boundary condition of the system, it is inevitable that the system should have ended this stage of development in an unstable supersaturated state designated schematically by point, *U*, on Fig. 1. There would therefore be a thermodynamic pressure on the system to increase the entropy production. This was accommodated by a series of fluctuations producing internal constraints. The first primitive colloidal systems envisioned by Oparin were the result of a series of such steps, the constraints being represented by internal and external surfaces. Of particular importance at later stages was the entry into symbiotic relationship of different primitive protoplasmic units through fluctuation. As Morgulis (1953) has noted, "the concatenation of chlorophyll, chloroplast and cytoplasm within the plant cell opened up new vistas of evolutionary potentialities by tapping the inexhaustible source of the sun's energy and making it available for biological progress." Such symbiotic units have new instabilities to which they respond by various morphological and oscillatory modes. Cell division, and reproduction in general, can be categorized as a response to such instabilities (*cf.*, Dean and Hinshelwood, 1964). The character of these self-reproducing entities epitomizes beautifully the tendency for a system to approach the stability point by compromising a tendency towards "dynamic efficiency" [(Prigogine, 1955) minimum entropy production through the photosynthetic process] and "chemical imperialism" [(Russel, 1927) maximum entropy production through cell division].

The evolution of the plant kingdom consists of the hierarchical continuation of symbiotic associations. Each addition of constraints through fluctuation results in new instabilities which led to morphological development and to periodic kinetic modes. The dendritic (morphologically unstable) external form of plant life may be regarded as a response to the tendency of the system to increase its entropy production. It is the essential thermodynamic character of the plant kingdom that it form a relatively stable ecosystem with the sun's radiation and the earth's mantle and that as a whole its "dynamic efficiency" dominates its "chemical imperialism" to yield a net accumulation of free energy. The carboniferous age with its vast accumulation of free energy represents the most constructive era of evolution since during that period the ecosystem was most successfully "bucking the second law" (Lindsay, 1959).

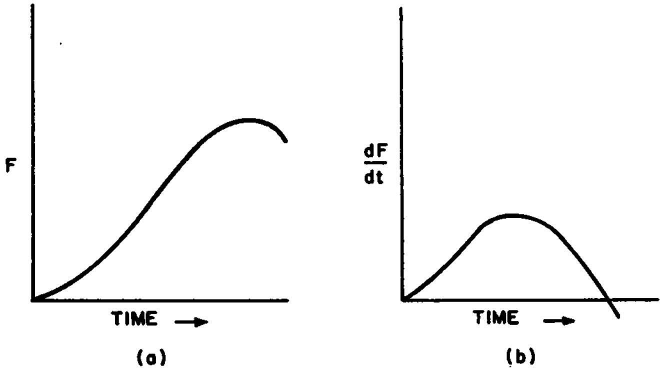
The course of evolution took a qualitative change in direction with the advent of the animal kingdom for the character of the ecosystem underwent a revolutionary change. In effect, the direct free energy source is no longer the sun but the free energy conserved by the dynamically efficient processes of the plant kingdom.[8] From the approximate theoretical point of view this may be regarded as a constant source of free energy so that the entropy balance and external constraints of the ecosystem of the animal kingdom are of the same form as previously. However, since photo processes are of minor consequence, the entropy flux term may be replaced by a free energy flow term. The balance now becomes, in terms of free energy,

$$\frac{dF}{dt} = (J_F)_i - (J_F)_o - T\frac{d_iS}{dt} \tag{3}$$

where J_F is the isothermal flow of available (free) energy into or out of the ecosystem as food for the herbivores or their primitive ancestors (metazoa).

Subsequent evolution consisted of the development of hierarchies of ecosystems, each being built upon the free energy products of the evolutionary predecessors. This may be thought of as the coming of age of chemical imperialism for populations came to fill every niche of available free energy and to degrade that energy to the best of their abilities. This imperialism has been culminated in the activities of man who extended his domain (and his ecosystem) not only to the free energy stores of the living plant and animal kingdom but to the prehistoric stores in the carboniferous beds, to the solar sources in the form of hydroelectricity, and to the ultimate source of solar energy in the nucleus.

If this conception is correct, the evolutionary history of the earth as indexed by the total free energy of the ecosystem and by the rate of production of free energy may be of the form shown in Fig. 2. As long as prehistoric and nuclear sources of energy remain, the free energy can continue to decrease without adverse effect



(a) (b)

FIGURE 2 Schematic temporal evolution of the earth's free energy resources (*a*) *F*(*c*) (*b*) *dF*/*dt*.

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[8] Actually, the animal kingdom is not the sole occupant of this ecosystem. Plants themselves, make direct use of the stored free energy accumulated by other plants and plant parasites occupy a sizeable niche as well.

on man's ecosystem. Furthermore, the improved efficiency of harnessing of the sun's non-biological effects (sunlight, hydro, winds, etc.) will provide an increasing source of free energy which lies outside the scope of Fig. 2.

It should be emphasized that as each new ecosystem is brought into play through a fluctuation which produces an evolutionary change, the surface of entropy production which applies to this subsystem must be chosen so as to accommodate the new effective constraints. Thus, the master potential surface for the earth spawns a myriad of overlapping subsurfaces corresponding to a series of overlapping spatial and energetic domains. In noting this we simply recognize that a new internal constraint for the whole system which occurs through fluctuation can be viewed formally as an external constraint for a subsystem.

The end point of evolution in a given ecosystem is stability corresponding to the saddle point of the potential surface. In view of the wide range of stable environments provided it is not surprising that a number of evolutionary branches have substantially attained this state (*e.g.*, the mollusks). This is the exception, however, since the majority of species (particularly the mobile land varieties) always have a variety of new ecosystems into which to evolve and are always subject to invasions from adjacent or overlapping ecosystems. In such circumstances one may only look for broad stability of a class (*e.g.*, mammals) as a whole, rather than of individual species. It does, indeed, appear that the mammals in the northern hemisphere have long since achieved over-all stability as had the marsupials in Australasia. With physical attributes perfectly adapted to every corner of the ecosystem, there were few channels left for change which did not duplicate existing attributes. Nature, in its fluctuating search did, however, find two attributes not previously fully exploited—manual dexterity and brain power, and these ultimately extended the dominion of *Homo sapiens* over all existing sources of free energy.

GENES AS THERMODYNAMIC CONSTRAINTS

We are greatly handicapped in understanding the evolution of the genetic mechanism because its antecedents were undoubtedly quickly eliminated through competition. We must, however, agree with Oparin that there was a long and complicated evolution up to this state. It is easily conceivable that there was a series of mechanisms of increasing complication which were capable of self-duplication—indeed many inorganic systems show spontaneous responses to unstable internal conditions which are analogous to this behavior. The most significant of these evolving mechanisms must have contained a photosynthetic element which provided a reaction product of ever increasing free energy content as a raw material for subsequent stages. The increasing complication of the raw material of evolution provided an increasing variety of possible new internal constraints and regression paths which through fluctuation allowed the system to express its tendency to move towards its stability point. We imagine a successful path on the potential surface (Fig. 3) as consisting of regressions towards temporary minima followed by upward fluctuations which opened regression channels towards more stable minima, and so on. The upward processes involved the introduction of new internal constraints whereas the regressive processes involved increasing complication of morphology and efficiency of the synthetic processes with the latter dominating over all. Naturally, many such paths by fluctuation would lead to less stable and therefore, untenable, states or to metastable *cul-de-sacs,* just as in the evolutionary history of advanced forms within the record of paleontology.

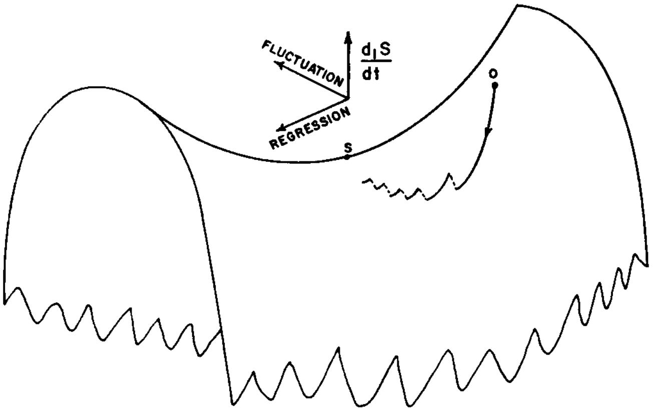

FIGURE 3 Schematic evolutionary path on the entropy production surface.

As the size and complication of the reaction products increase the possibility of a qualitative change in the character of the internal constraints appears—for as the surface area of certain molecules increase they appear more and more to the smaller and more mobile reacting molecules as an invariant constraint of the system. Such constraints, however, are qualitatively different from membranes or phase interfaces in inorganic systems since their interactions with the mobile surroundings can now be specific rather than random through variation of its surface properties from point to point. This specificity of the internal constraints opened up completely new vistas of evolutionary development which were culminated in the living cell and the genetic mechanism of evolution. The fact that the reproductive and regulative mechanisms based on the DNA molecule appears to be operative with only quantitative variations within all levels of the biosphere suggests that the cellular structure represents a dead end in the search for stability. Within its membrane and nutrient environments it has achieved as close to the minimum possible entropy production but it still lies slightly below the saddle point. The resulting instability is manifested in its cyclic tendency to divide in an unsuccessful attempt to achieve the ultimate stability point. With this high degree of stability further evolution could only occur by entry into symbiotic relations.

THEORY OF NATURAL SELECTION AND THERMODYNAMICS

There is a considerable conceptual difficulty in bringing the thermodynamic method as outlined thus far to bear upon an evolutionary subunit smaller than a class. The reason is that the ecosystem of each small subunit (which includes all genetic material as part of the boundary conditions) is inextricably mixed with that of other subunits making it almost impossible to identify fixed boundary conditions for a steady state model. This mixing of ecosystems is strongly related to natural selection, which is at the core of classical discussions of evolution. This mixing of macroscopic units gives rise to a new type of statistical ensemble which if sufficiently random becomes amenable in principle to mathematical analysis.

A perfect analogue is to be found in fluid mechanics. At low dissipations the statistical elements are taken as molecules and a satisfactory phenomenology of laminar (streamlined) flow can be based thereupon. As the dissipation rate increases, instabilities arise, resulting in nucleation of vortices. Ultimately, at high dissipation, these vortices become so numerous and so random in their interactions that they define a new statistical ensemble upon which a theory of turbulent flow can be erected (Onsager, 1949). It is our opinion that the genetical theories of natural selection due to Fisher (1930), Haldane (1932), and Wright (1942) can be classified in this way. Were such "mechanical" theories developed to sufficient perfection it is conceivable that they could generate the potential function for change and thus obviate the need for the ill defined sense of progress contained in words like "adaptation" and "fitness." This potential function should correspond to that introduced here on the basis of molecular chemistry.

DEVELOPMENT OF THE BIOLOGICAL INDIVIDUAL

If it is accepted that thermodynamic potentials control the evolutionary history of the race, it follows that they also act to control the history of the individual. Prigogine (1955) has already noted the tendency of the adult individual to minimize its rate of metabolism per unit volume (entropy production) as it approaches the adult (steady)state. We will now amplify and modify this statement by noting the over-all tendency for the extension of the dominion over free energy sources as adulthood is approached accompanied by an improved dynamic efficiency of all the processes. We can represent its biological history schematically on the potential surface as in Fig. 4. The individual through growth by a series of constraint producing fluctuations (*e.g.*, cell divisions) from point *O* to *A* has tended to maximize its entropy production, but in achieving that state it lies in a state which is a minimum with respect to virtual changes in its process parameters with fixed internal constraints (Onsager's minimal principle). The normal process of aging has been conceived of as cumulative genetic injury which corresponds to a gradual release of the internal constraints and a corresponding decrease in the entropy production as the system

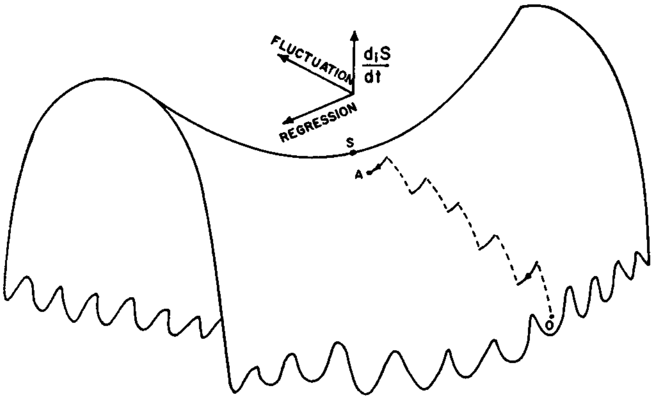

FIGURE 4 Schematic path for aging of the individual on the entropy production surface.

migrates away from the stability point. Ultimately a constraint is released which allows unhindered regression and leads to that state of zero entropy production rate which is death.

It is our contention that the potentials act not only on the system as a whole but within each identifiable ecosystem within the hierachy of structure. Indeed, we believe that they provide a possible key to the understanding of the spontaneous causal relations in genetic regulation and morphogenesis.

It has been proposed that specificity can be understood on the basis of short and long range molecular interactions (Waugh, 1961). While this view may be tenable for certain simple crystallization reactions, such relations are completely inadequate to the general problem of morphology. Specificity in biological systems has both static and kinetic aspects which must always be considered in relation to each other. Weiss (1959) has, for example, emphasized that cell morphology is strongly sensitive to environment as well as to its molecular structure. To quote Schmitt (1959) "the genetic code may be thought of as arranging for the biosynthesis of the complex macromolecules of many kinds, but interactions of the macromolecules under specified conditions occurs spontaneously." It is this spontaneous reaction subject to the external and molecular constraints which represents the regulative and morphogenetic processes of the system. The information for development comes not only from the static relations of the genetic map and the boundary conditions but is flowing into a dissipative system as nutritive free energy (Schrödinger, 1948). It is the combination of the two which yields the organization of the biosystem. It seems to us that it was an incorrect assessment of this latter contribution which led to a failure of Elsasser's (1958) information balance for a biological system and which led him as a result to postulate "biotonic" laws acting in addition to the physical laws of organic processes.

COMMENTS ON LOTKA'S PRINCIPLE

As noted earlier, Lotka arrived at a viewpoint which is substantially the same as ours on empirical grounds. As an example, we present the following quotation. "It has been remarked that the influence of living organisms is to retard the dissipation of energy. So far as the plant world is concerned this seems essentially true. Green plants act as accumulators storing sunlight which would otherwise shortly be converted into heat at terrestrial temperatures.

But the influence of animals is essentially in the opposite direction, since their activities are conducted with dissipation of energy, catabolism exceeding anabolism.

At first sight there is something preplexing about these two opposing tendencies. But this perplexity exists only so long as we seek to express the drift of organic nature in terms of a retardation or a promotion of the dissipative process. As soon as we frankly accept the fact that both are going on side by side the perplexity vanishes."

Lotka goes on to formulate his principle as follows: "A simile may be helpful in illustrating the situation. Consider a reservoir constructed to collect rainwater. Now let there be two agencies at work, one tending to enlarge the catchment area, the other tending to enlarge the outlet or outlets from the reservoir. In one sense these two influences seem antagonistic, one tends to increase the volume of water in the reservoir, the other tends to decrease it. But in one thing they cooperate: *Together they increase the total flow through the reservoir.*" His final formulation states that "Evolution . . . proceeds in such a direction as to make the total energy flux through the system a maximum *compatible with the constraints.*" He is here using the term energy as a contraction for "available" energy which for an isothermal, isobaric system is the Gibbs' free energy. We thus see that the analogue chosen was an unfortunate one. Whereas water flow through a system as conceived by Lotka is a conservative quantity, free energy flow is not, as indicated by equation 3. Thus the term "energy flux through the system" has no meaning since the inlet and outlet fluxes have different values in general. The proposed principle must therefore be rejected. This criticism should not, however, detract from the uncanny insight which Lotka has gained through empirical inference and an inadequate theoretical model.

DISCUSSION

It appears to us that the present contribution represents a necessary continuation of the views of Boltzmann, Ostwald, Russel, Schrödinger, Lotka, Blum, and Prigogine and Wiaume on the role of thermodynamics in the development of organic matter. It was the latter authors who first brought the powerful synthetic methods of irreversible thermodynamics as exemplified by the principle of minimum entropy production to bear upon this problem. It is our premise that Prigogine's macroscopic regression principle speaks to only part of the problem and that this in combination with Onsager's microscopic fluctuation theorem, containing both a maximal and minimal statement, is a necessary part of the synthesis. Furthermore, we have found it necessary to postulate that Onsager's microscopic maximal principle has a counterpart which indexes the approach of an ecosystem towards stability *via* a series of fluctuations which introduce new constraints into the system. These constraints take the form of internal surfaces of both specific (genetic) and non-specific (membranal) character.

The potential functions for terrestrial processes therefore takes the form of a saddle surface in a configuration space of innumerable coordinates, both microscopic and macroscopic. Terrestrial evolution consists of the motion of a configuration point towards the stable saddle point of the surface. The extreme variety of the working material and the complexity of the external boundary conditions assures that the search for stability will be a long, if not infinite one. It is particularly satisfying that the form of the potential is such as to provide a synthesis of two apparently conflicting tendencies—the tendency towards complication (which is a corollory of the minimal principle, Prigogine, 1955) and towards high dissipation (which is the maximal principle). The evolutionary path represents a compromise between these two, a character which can be recognized at all levels of the biosphere.

We emphasize here that the use of potential functions is an interim procedure in the search for a detailed understanding of the cooperative processes involved in heterogeneous transitions. Like equilibrium thermodynamics, the potential method concerns itself only with the temporal ordering of states, and avoids consideration of the much more complex problem of rate of transition between states. Detailed kinetic theories will be required for this stage of advance.

It must be admitted that the linear theory of irreversible processes upon which this principle is based is a very bad approximation, particularly where applied to chemical processes which involve large free energy changes. Considerable progress has already been made in extending the formalism into these domains (Prigogine, 1955; Glansdorf and Prigogine, 1964; Li, 1962). It is our view, however, that such quantitative advances can only cloud the issue in an area where qualitative answers must first be sought.

This formalism should first find its application as an aid to classifying the diverse phenomena of evolution. For example, a cursory review of the terminology of the discipline (Simpson, 1949) suggests that terms with a kinetic sense fall into two groups, one implying a tendency to increase the rate of entropy production and the other to decrease it.

There does not appear to be much prospect for an experimental program applying these ideas to the processes of evolution. The most attractive arena for investigation is in the study of the regulatory processes and morphogenetic development of the living individual or of some ecosystem within the living system. The methods of Selye (1956, 1958) and Weiss (1959) in which the external or internal conditions are controlled are signposts in the direction of thermodynamic understanding. These experiments are analogues of the controlled inorganic processes described in our papers A, I to IV.

It is inevitable that a principle of this generality should suggest application to the evolution of human society and to the behavior of the individual. We can only note here that the ideas that arise naturally are not incompatible with the views of Herbert Spencer, Bertrand Russel, and Julian Huxley.

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