A THERMODYNAMIC THEORY OF THE ORIGIN AND HIERARCHICAL EVOLUTION OF LIVING SYSTEMS

by H. J. Hamilton

Abstract. Growing interest in the origin of life, the physical foundations of biological theory, and the evolution of animal social systems has led to increasing efforts to understand the processes by which elements or living systems at one level of organizational complexity combine to form stable systems of higher order. J. Bronowski saw the need to extend or reformulate evolutionary theory to deal with the hierarchy problem and to account for the evolution of systems of "stratified stability." The hierarchy problem has become a matter of great interest also in nonequilibrium thermodynamic theory.

An effort is made here to develop an abstract, phenomenological model, based on the laws of thermodynamics, to account for the origin and hierarchical evolution of living systems. It is argued that the principle of minimum entropy production, developed by I. Prigogine, applies generally to all thermodynamic systems and processes and is implicit in an extended and more complete formulation of the second law of thermodynamics. From this are derived a thermodynamic criterion and a principle of thermodynamic selection governing the formation of stable systems of "elements" of various levels of organization. Thermodynamic selection gives rise to the creation of "elements" having increasingly "open" characteristic structures which may combine spontaneously to form "social" or crystalline systems capable of growing and reproducing themselves through processes of fissioning or budding. Such simple, self-reproducing systems are capable of evolving by natural selection, which is seen to be a special case of the more general process of thermodynamic selection. 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. Some implications of this open-ended model and opportunities for testing its empirical and theoretical utility are explored.

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Despite important advances in recent decades, evolutionary theory remains largely isolated from the laws of physics and chemistry and has yet to account for the origin of life, the emergence of multicellular organisms, and the evolution of social systems of organisms, including those of humankind. This is not surprising since evolutionary theory has been concerned for the most part not with the emergence of new hierarchical levels of organization but with developments occurring within a single level.[1] Darwin, it should be noted, was not unmindful of these larger problems. With remarkable prescience he speculated in his later years about the biochemical origin of life and the possibility that "the principle of life will hereafter be shown to be a part, or consequence, of some general law. . . ."[2]

While some may yet argue to the contrary, it appears that questions having to do with the physical foundations of biological theory and the organization of living systems in hierarchical structures may be of central importance in evolutionary theory. Indeed, it would appear that the much-debated question of reductionism is intimately related to the hierarchy problem, which is essentially this: How and in conformance with what fundamental laws do elements at one level of organizational complexity combine spontaneously to form stable elements of a higher order and in so doing yield some measure of their freedom of movement or behavior to constraints imposed by the higher-order unit?

The hierarchy problem and the issue of reductionism have received considerable attention in recent conferences and publications.[3] These problems have been approached also from the viewpoint of nonequilibrium thermodynamic theory.[4] However, the hierarchy problem remains unresolved, and the fundamental processes which have given rise to progressively higher levels of organization in the biosphere remain obscure.

Evidently, as J. Bronowski and others have suggested, there is a need to formulate evolutionary theory in a more fundamental and comprehensive way in order to deal with these larger questions.[5] That is my aim in this paper. In particular I will seek to develop an abstract, thermodynamic model to account for the origin and hierarchical evolution of self-reproducing systems and to explore some implications of this model and possibilities for testing its empirical and theoretical utility.

A Thermodynamic Model of Evolution

In the following I shall (1) present the fundamental thermodynamic arguments upon which the proposed model rests, (2) discuss the general concepts of "elements" and "affinities" between elements, (3) derive a general principle of thermodynamic selection, (4) show how simple, self-reproducing "crystalline" systems may emerge through processes of thermodynamic selection, (5) argue that the principle of natural selection is a special application of the principle of thermodynamic selection and therefore may be given a more fundamental and quantitative expression, (6) discuss alternative ways in which relatively simple, self-reproducing systems may evolve into more complex and highly organized systems, and (7) show how such systems may come to serve as "elements" or building blocks in the creation of self-reproducing systems of a higher order and in this way give rise progressively to hierarchical systems of increasing size and complexity.

PRINCIPLES OF NONEQUILIBRIUM THERMODYNAMICS

The thermodynamics of irreversible processes has received growing attention since the pioneering work of L. Onsager.[6] Onsager showed that Rayleigh's "principle of the least dissipation of energy" could be generalized to account for linear irreversible processes of heat conduction in anisotropic crystals. In particular he showed that the second law of thermodynamics requires that the dissipation function $\phi = (1/2T) \Sigma R_{ik} J_i J_k$ characterizing such processes be minimum in the stationary state. At a later date I. Prigogine developed the principle of minimum entropy production, which states that the rate of entropy production in an open or closed thermodynamic system, characterized by linear irreversible processes and subject to unchanging external parameters, is constant and minimal in the stationary state.[7] (Thermodynamic systems are considered to be isolated if no exchange of energy or materials is permitted with an external environment, closed if energy but not materials may be exchanged, or open if both energy and materials may be exchanged.) In the stationary state, $\dot{S} = \dot{S}_e + \dot{S}_i = 0$ and $-\dot{S}_e = \dot{S}_i > 0$, where $\dot{S}$ is the rate of change of the entropy of the system, $\dot{S}_e$ is the entropy flow between the system and its environment, and $\dot{S}_i$ is the rate of entropy production resulting from irreversible processes within the system. The entropy production of a system is given by $\dot{S}_i = (1/T) \Sigma J_i X_i$, where T is the absolute temperature and J_i and X_i are the thermodynamic flows and forces, respectively characterizing the irreversible processes. Prigogine proved that $\dot{S}_i$ has a constant, minimum value in the stationary state for systems in which the thermodynamic flows and forces are linearly related and the Onsager reciprocal relations, $R_{ik} = R_{ki}$, hold.

I. Gyarmati has developed a more general formulation of the variational principle employed by Onsager from which may be derived all of the conditions characterizing the stationary state, including the linear relationships between fluxes and forces, Onsager's reciprocal relations, the principle of least dissipation of energy, and the principle of minimum entropy production.[8] It is important to emphasize here that this theory is restricted to the analysis of systems in which linear irreversible processes operate and, therefore, in general to systems which are not far removed from the equilibrium state.

Lately there has been a growing concern to extend the theory of nonequilibrium thermodynamics to deal with a variety of important problems involving nonlinear irreversible processes. P. Glansdorff and Prigogine have sought to extend the theory of entropy production in open systems and to determine how fluctuations occurring in nonlinear, irreversible processes may give rise to stationary states that are increasingly distant from equilibrium and characterized by progressively higher rates of entropy production and lower values of entropy.[9] Their aim is thus to develop a general thermodynamic theory to account for the evolution and stability of such "dissipative structures." Prigogine, G. Nicolis, and A. Babloyantz have focused their attention in particular on the problem of biological evolution.[10] They argue that an increase in dissipation is possible for nonlinear systems driven far from equilibrium and that such systems may be subject to a succession of unstable transitions which lead to spatial order and to increasing entropy production. These authors believe that such transitions toward increasing dissipation were essential to prebiological evolution, as indeed the creation of stable systems of increasing size and decreasing entropy implies.

These arguments on the evolution of stable systems reflect a central concern with nonlinear irreversible processes operating in open thermodynamic systems and with the role of fluctuations in effecting transitions from lower- to higher-level stable states. Here an alternative approach will be presented which argues that (1) the principle of minimum entropy production holds generally for all thermodynamic systems and processes and is implicit in an extended formulation of the second law and (2) the spontaneous creation and hierarchical evolution of all ordered structures in a thermodynamic system are the result of irreversible processes which proceed at each stage in such a manner as to minimize the entropy production of the system, consistent with external constraints. The assumption of nonlinear processes is therefore not an explicit or necessary condition for the evolution of such structures, though nonlinear processes may play an important role in determining the specific form, pattern of development, and behavior of such systems.

As yet it has not been rigorously demonstrated that the principle of minimum entropy production holds generally for all thermodynamic systems and irreversible processes, though A. I. Zotin has argued the plausibility of this assumption on the basis of Le Chatelier's principle of moderation and believes that the principle should be regarded as the fourth law of thermodynamics.[11] However, it would appear that the principle of minimum entropy production is intimately related to the assumption that an isolated thermodynamic system must evolve toward a state of equilibrium and therefore may be implicit in any expression of the second law which formally incorporates this assumption.

The second law states that the time rate of change of entropy in an isolated thermodynamic system is either zero or positive, that is, $\dot{S} \geqslant 0$, with the equality sign applying to the condition of thermodynamic equilibrium. The "local formulation" of the second law, which is due to Prigogine and derives from the fact that entropy production is an extensive property of a thermodynamic system, asserts that the entropy production in every macroscopic region of a thermodynamic system is either zero or positive. (A macroscopic region of a thermodynamic system, according to Prigogine, is any region containing a number of molecules sufficiently large for microscopic fluctuations to be negligible.) Thus, if $\dot{S}_j$ is the entropy production in a macroscopic region or cell of a thermodynamic system, then the local formulation requires that $\dot{S}_j \geqslant 0$ in all regions or cells of the system. The equality holds for all cells which are in a state of equilibrium, while the inequality holds for all cells in which irreversible processes occur.

The entropy production in an isolated thermodynamic system is therefore

$$\dot{S} = \sum_{j=1}^{n} \dot{S}_j \geqslant 0 ,$$

where $\dot{S}_j \geqslant 0$ for all $j = 1, 2, \ldots, n$ and n is the total number of cells of the system. What remains undetermined or undefined in this formulation of the second law is the sign of each $\ddot{S}_j$ and of $\ddot{S}$ at any time for systems which are not initially in a state of equilibrium, that is, whether the rate of entropy production in each cell and in the system as a whole increases or decreases with time. Indeed, the above formulation of the second law imposes no explicit requirement that an isolated thermodynamic system approach a state of equilibrium, that is, that $\dot{S}_j \rightarrow 0$ for all cells as the system ages. However, empirical evidence indicates not only that an isolated thermodynamic system will evolve toward a state of equilibrium but that it will do so in such a manner as to cause the mean entropy production in the system (allowing for the possibility of fluctuations or damped oscillations) to decrease monotonically. This implies that the approach to equilibrium at all times, neglecting fluctuations or damped oscillations, must satisfy the condition $\ddot{S}<0$.

The above "equilibrium assumption," which is implicit in classical and statistical thermodynamic reasoning, suggests the need to extend the formal expression of the second law as follows: The entropy function in any isolated thermodynamic system, neglecting fluctuations or damped oscillations, must satisfy the conditions $\dot{S}\geqslant 0, \ddot{S}\leqslant 0$, where the equality signs hold in the state of equilibrium and the inequalities characterize the approach to equilibrium. The principle of minimum entropy production is implicit in this extended formulation of the second law and therefore would appear to apply generally to all thermodynamic systems and processes.

Since fluctuations or damped oscillations in the entropy production of a thermodynamic system will play no fundamental role in the general theory to be developed, I shall omit the above qualifying statements in the remaining discussion. However, this is not to suggest that macroscopic fluctuations or damped oscillations may not have great significance in more detailed studies of the evolution of thermodynamic systems.

It should be noted here that all derivations of the second law from classical, statistical mechanical, or astrophysical thermodynamic arguments are based on one or another axiomatic or a priori assumption about the nature of the universe.[12] The above equilibrium assumption and the principle of minimum entropy production implied therein constitute an a priori assumption about the composition and behavior of matter in the universe, namely, that irreversible processes always give rise simultaneously to the destruction and creation of ordered structures in the universe and in such a manner as to cause the entropy to increase at a minimal rate.[13] The implication is that irreversible processes are never perfectly entropic, that is, they never lead solely to the production of entropy. If this reasoning is correct, then it would be necessary to conclude not only that it is impossible to convert heat energy completely into mechanical energy in any irreversible process but that it is likewise impossible completely to degrade available free energy in any irreversible process. No heat engine can operate with 100 percent efficiency or with zero efficiency. In all cases some "useful" work will accompany the degradation of available free energy, that is, some ordered structure or behavior will result. Here the notion of "order" or "structure" appears to be intimately related to the arrangement of matter in such a way as to minimize the entropy production of a thermodynamic system. Alternatively, we may conclude that, just as it is not possible for a Maxwellian Demon to order an initially unordered system, so it is not possible for an ordered system to degenerate spontaneously into a disordered system without creating in the process a Maxwellian Demon, that is, an ordered, discriminating structure, somewhere in the system. Information cannot be obtained without dissipating available free energy, nor can available free energy be dissipated without producing some finite amount of information in the form of ordered, physical structures as a by-product.

A simple illustration of these ideas, derived from H. Morowitz, is presented in figure 1.[14] The illustration depicts the spontaneous crea-

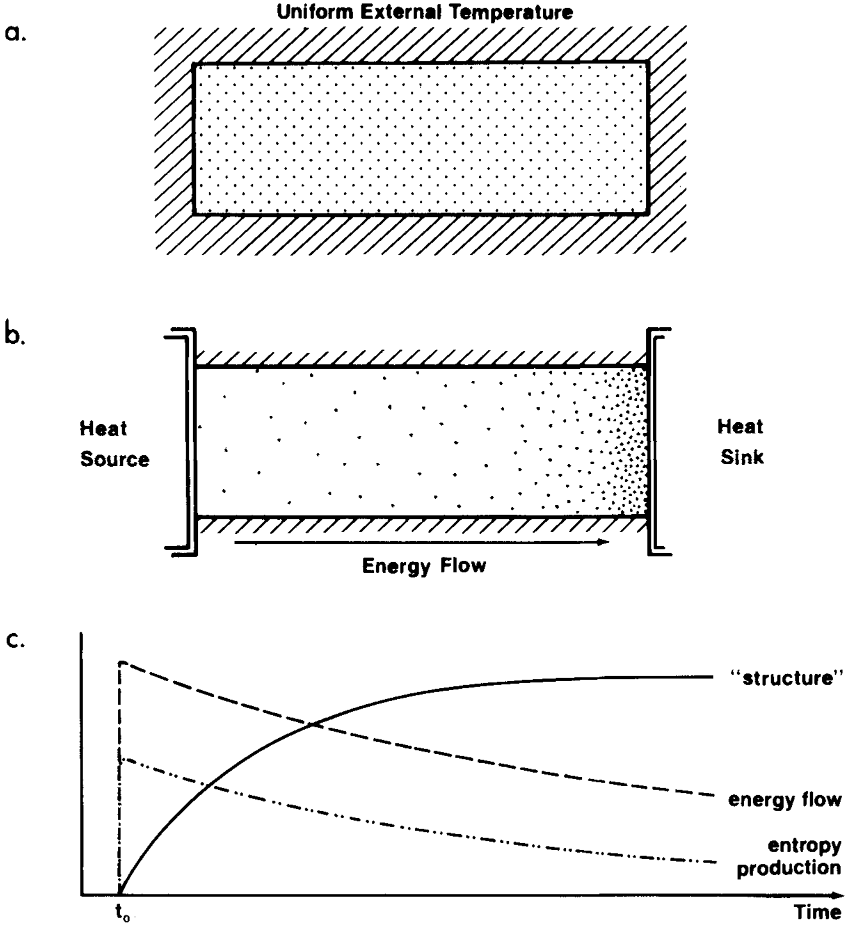

FIG. 1.—Spontaneous creation of "structure" in an ideal gas, initially in a state of equilibrium (*a*), due to energy flow resulting from application of a quasi-constant external thermal force at time t_0 (*b*); measures of "structure" of gas, energy flow through, and entropy production in the gas (*c*).

tion of order or "structure" in an ideal gas by the flow of energy through the system, resulting from the sudden application of a quasi-constant external thermal force. The structure thus created serves to decrease the rate of energy flow through and entropy production in the gas to some minimal stationary-state levels and thereby to cause the total thermodynamic system—heat source, gas, and heat sink—to proceed toward an equilibrium state at a minimal rate. The decay of order and free energy in the external environment of the gas is accompanied and partially offset by the creation of order and free energy in the gas. The formation of more stable chemical structures in closed and open thermodynamic systems is brought about in essentially the same way. All such structures may be thought of as more or less complex and stable Maxwellian Demons which evolve spontaneously from the flow of energy and materials from one macroscopic region of a thermodynamic system to another.

The proposed extended formulation of the second law requires that any increase in the rate of entropy production that may occur in one or more macroscopic regions of an isolated thermodynamic system be more than offset by decreases in the rate of entropy production elsewhere in the system. That is to say, the state of thermodynamic forces and fluxes in an isolated, nonequilibrium thermodynamic system must evolve in such a way as to cause the entropy production of the system as a whole to decrease monotonically.

This requires in particular that the entropy production in any macroscopic region of an isolated thermodynamic system subject to constant (or, more accurately, quasi-constant) external constraints decrease monotonically toward some minimal, quasi–stationary-state value. The state of thermodynamic forces and fluxes in the region must evolve through irreversible processes so as to minimize at all times, neglecting fluctuations, the entropy production in the region and therefore in the thermodynamic system as a whole.

The foregoing suggests that the local formulation of the second law is incomplete since it imposes no requirement that an isolated system evolve toward a state of equilibrium. However, a modified local formulation of the second law, which incorporates the equilibrium assumption, may be stated as follows: In any macroscopic region (subject to constant external constraints) of a thermodynamic system, the entropy production is either zero or positive and the time rate of change of entropy production is either zero or negative, or $\dot{S}_j \geqslant 0$, $\ddot{S}_j \leqslant 0$. Alternatively, we may say that in every macroscopic region of a thermodynamic system subject to constant external constraints the specific entropy production σ, that is, the entropy production per unit mass or volume, is either zero or positive and the time rate of change of specific entropy production, neglecting fluctuations, is either zero or negative, or $\sigma \geq 0$, $\dot{\sigma} \leq 0$.

For closed thermodynamic systems subject to constant external constraints (with which I shall be concerned centrally), the above statement is equivalent to saying that the system will evolve, through the spontaneous creation of ordered structures, in such a manner as to lead to a minimal, stationary-state value for the entropy production of the closed thermodynamic system as a whole. Thus presented, the modified local formulation of the second law, with its implicit generalization of the principle of minimum entropy production, will serve as the basis for the development of a phenomenological theory to account for the origin and hierarchical evolution of living systems on earth.

FORMATION OF STABLE STRUCTURES IN A CLOSED THERMODYNAMIC SYSTEM

Since the notion of an ordered structure or system implies the existence of stable relationships, affinities, or bonds between elements or entities, it would be helpful if we could formulate our ideas of interelement affinities and systems stability in some general or broadly applicable way. The aim here will be to extend the concepts underlying the quantum theory of chemical affinities and the formation of stable molecular complexes to apply to the formation of stable systems of higher-order "elements" and entities.

Chemical affinities derive from the exchange or sharing of electrons between atoms having incomplete outer electron shells. More or less stable molecular structures may be formed, under suitable conditions, to the degree that such configurations lead to a more probable quantum state for each element involved. Unfortunately, our capacity to deal with complex structures in this way is as yet very limited. However, thermodynamic theory provides us with an alternative approach. Thus we know that in an isolated, multicomponent thermodynamic system chemical reactions will proceed in such a way as to lead to an equilibrium state characterized by maximum entropy, minimum free energy, and zero entropy production. Moreover, the principle of minimum entropy production tells us that in a closed thermodynamic system chemical reactions will lead to a stationary state characterized by minimum entropy, maximum free energy, and minimum entropy production. That is to say, two or more elements will tend to combine in a stable configuration, under specific thermodynamic constraints, to the extent that such association contributes, on the average, to a decrease in the entropy production of the total system.

Let us now formulate these ideas in a more general way so that they may be applied to more complex entities and stable systems of entities. We shall say that an "element," "entity," or "system" is any complex (generally composed of simpler components) whose identity or characteristic structure remains essentially unchanged in some time frame and in the course of interactions or associations with other such elements or entities. This implies that the bonds holding the components of the elements together are relatively more stable and stronger than the bonds which may form between elements. The characteristic structure of an element determines its stability in the free state and affinity for other similar or dissimilar elements. Any element whose structure is "closed" in the sense that it may not adapt to conditions in the environment, and in particular to the structural configurations of other elements, in such a way as to decrease the total entropy production may be said to be inert or nonreactive, while the opposite holds for elements having "open" or adaptive structures. When different or similar kinds of reactive elements combine, we shall speak of "symbiotic" or "social" affinities, bonds, relationships, associations, or systems, respectively. In general, symbiotic systems will be limited in size, that is, in the number of constituent elements, due to the decreasing number of options for structural coadaptation with the addition of each new and different element. Interactions or associations between elements involve the exchange or sharing of some structural component or property of the elements and some mutual accommodation of their characteristic structures.[15] Interactions among elements in an isolated thermodynamic system will proceed in such a way as to lead to an equilibrium state characterized by zero entropy production, minimum free energy, and maximum entropy, while interactions among elements in a closed thermodynamic system will lead to a stationary state characterized by minimum entropy production and total entropy and maximum free energy, under given constraints. In the latter case, two or more elements will form a stable association to the degree that such association contributes, on the average, to a decrease in the entropy production of the total system.

In anticipation of later discussion I shall suggest that these propositions apply not only to atoms, monomers, and polymers as elements but to self-reproducing cells and protocells, multicellular organisms, and social systems of organisms whose identity or characteristic structure remains essentially unaltered by interaction or association with other similar or dissimilar cells, organisms, or social systems. The affinities among atoms, monomers, and polymers involve the exchange or sharing of electrons, or weak coulomb forces between polarized units; while the symbiotic or social affinities among cells, multicellular organisms, and social systems of organisms may involve the exchange or sharing of energy, materials and information resources, or produced "goods" and "services." Such bonds may be relatively strong or weak, and stable associations or systems may result from a few strong bonds or many weak bonds. The latter appear to be of increasing importance in determining the stability and potential for structural change or adaptation in the evolution of more complex elements and systems. This line of reasoning suggests that the process by which stable organized systems, including living systems, are created may be explained most satisfactorily in terms of a general quantum theory of the affinities between elements and its phenomenological counterpart derived from the principle of minimum entropy production.

THERMODYNAMIC SELECTION

If elements or entities may combine in alternative compositional and structural forms in closed thermodynamic systems, what determines the relative frequency or population density of such systems under given constraints? Since all such systems are formed spontaneously from limited numbers of elements, there exists in effect a competition for available elements, and we should expect that the populations of variant forms of systems would be determined by some sort of selection process. Presumably the frequency distribution of such systems could be computed if we had a sufficient knowledge of their micro states. However, in lieu of this capability, we must approach the problem from a different perspective.

The principle of minimum entropy production permits us to formulate the selection criteria in terms of the probability that the formation of a particular system of elements will result in a decrease in the entropy production of the total thermodynamic system. Since entropy production is an extensive property of a thermodynamic system, we may reason that two elements will tend to combine under given conditions if, on the average, the entropy production of the complex $\dot{S}_c$ is less than the sum of the entropy production of each free element $\dot{S}_a$ and $\dot{S}_b$, or $\dot{S}_c < \dot{S}_a + \dot{S}_b$. More generally we may say that an element will bond to an existing complex of elements if the increase in entropy production $\Delta\dot{S}_c$ of the complex, resulting from the addition of the element, is less than the entropy production of the free element, or $\Delta\dot{S}_c < \dot{S}_a$.

This concept may be formulated more usefully in terms of the specific entropy production σ_c of the complex, that is, the entropy production per unit mass and the specific entropy production σ_a of the free element. The above inequality may then be written,

$(\sigma_c + \Delta\sigma_c)(M_c + M_a) - \sigma_c M_c < \sigma_a M_a$, where M_c is the mass of the complex, M_a is the mass of the free element, and $\Delta\sigma_c$ is the change in the specific entropy production of the complex resulting from the addition of the free element. From this we may derive the following thermodynamic criterion for the addition of an element to an existing complex:

$$\Delta\sigma_c < \frac{M_a(\sigma_a - \sigma_c)}{M_c + M_a} \quad \text{or} \quad \theta_{c,a} = \frac{M_a(\sigma_a - \sigma_c)}{M_c + M_a} - \Delta\sigma_c > 0\,,$$

where $\theta_{c,a}$ is a measure of the affinity of a complex c for a free element a. In practice the specific entropy production of an element or complex of elements may vary over a range of values, and it would be necessary in a more rigorous presentation to formulate these relationships in probabilistic terms. Thus the larger the value of $\theta_{c,a}$, the greater the probability that an element will be attached to the complex. If one or another of different kinds of elements $(a_1, a_2, \ldots, a_m)$ may bond to the complex to form new and different complexes, then that association for which $\theta_{c,a_i}(i = 1, 2, \ldots, m)$ is maximum will have the greatest stability and, other things being equal, will be produced most readily. In more precise terms we would say that the probability that a particular kind of complex will be formed by the addition of one or another kind of element to an existing structure, or alternatively that the frequency of occurrence of such a complex in a large population of such complexes, will vary directly, other things being equal, with the value of $\theta_{c,a_i}(i = 1, 2, \ldots, m)$.

If $M_c >> M_a$, the first term of $\theta_{c,a}$ approaches zero and differences in the mass or specific entropy production of the free elements a_1, a_2, $\ldots$, a_m may be insignificant in relation to the differences in the values of $\Delta\sigma_c$. Under these conditions $\theta_{c,a}$ will be maximum for that element for which the value of $\Delta\sigma_c$ is either maximally negative or minimally positive, and the above selection criterion may be reformulated as follows: 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 (where $M_c >> M_a$), or alternatively the frequency of occurrence of such a complex in a large population of systems thus formed, will vary inversely, other things being equal, with the value of $\sigma_{c,a_i}(i = 1, 2, \ldots, m)$. Here σ_{c,a_i} refers to the specific entropy production of the complex formed by the addition of an element a_i to an existing structure c. I shall refer to this formulation of the selection criterion as the principle of thermodynamic selection since it implies competition among different kinds of elements in the process of forming stable associations with other elements or complexes of elements. The principle of thermodynamic selection applies to all thermodynamic systems, whether characterized by linear or nonlinear irreversible processes. In the case of isolated thermodynamic systems the entropy production decreases, as the system ages, to a vanishingly small level. Consequently, in the equilibrium state the specific entropy production of all elements and complexes vanishes, along with the function $\theta_{c,a}$ for all complexes. Thus we see that affinities between elements and the formation of stable associations of elements are contingent upon energy dissipation and entropy production.

It will be apparent from the above that elements which are least stable in the free state have the greatest potential for combining in ordered structures and therefore for decreasing the entropy production of the total thermodynamic system. Thus elements that are inert or highly stable in the free state are singular products of the thermodynamic selection process in that their closed structures prevent them from serving as building blocks in the creation of higher-order systems and thereby contributing to a further decrease of total entropy production. A structure will be more or less open to the extent that the bonds holding the components together permit some relative motion or variation of the structural relationships between components. The larger an element (i.e., the greater the number of components), the more flexible the bonds between components, and the less stable it is in the free state, the more open and adaptive will be its characteristic structure. In general, such elements are created by the successive addition of identical or similar components in some repeating structural pattern or sequence, subject to the constraints imposed by the thermodynamic selection process. Openness or adaptability of structure is of central importance not only because it permits elements to combine under given conditions but because it enables an element or system to adapt to different or changing conditions in such a way as to maintain a minimum value of specific entropy production. A structure which may adapt so as to maintain a relatively low value of σ_c in different or changing environments will have a selective advantage over other similar but less adaptive structural forms, that is, it will have a relatively high frequency of occurrence in such environments.

FORMATION AND GROWTH OF "SOCIAL" SYSTEMS

As was noted earlier, the constraints on structural adaptation impose rather severe limits on the size of symbiotic systems and therefore on the possibilities for decreasing the entropy production of a thermodynamic system. Such limitations may be small or vanish in social systems which may grow by successive addition of identical elements in regular or repeating structural arrangements. We may refer to such social systems as "crystals" or "crystalline" systems.

Let us consider a closed, quasi–steady-state system containing identical free elements a and a growing crystal of these elements. We assume therefore a social affinity between the elements sufficient to bind them together in a stable crystalline configuration under the conditions imposed. By definition, the energy flux and entropy production of the thermodynamic system are approaching constant values and the total number of elements is conserved in the transfer of an element from the free to the bound state. From the principle of minimum entropy production we may reason that the crystal will continue to grow as long as the increase in entropy production, with the addition of each element, is less than the accompanying decrease in the total entropy production of the free elements. Indeed, the general thermodynamic criterion for the addition of an element to a complex applies to a growing crystal. That is, the crystal will continue to grow so long as

$$\theta_{c,a} = \frac{M_a(\sigma_a - \sigma_c)}{M_c + M_a} - \Delta\sigma_c > 0\ .$$

This criterion indicates that growth of the crystal may occur even when the addition of an element results in an increase in the specific entropy production of the crystal, providing that such increase does not exceed the value

$$\frac{M_a(\sigma_a - \sigma_c)}{M_c + M_a}\ .$$

As we shall see later, this possibility may have great significance for the development of a general theory of self-reproducing systems.

The possibility that the specific entropy production of a system might change with the addition of an element has been taken into account thus far only in a formal way. We should expect σ_c to vary somewhat with the addition of different kinds of elements, if only because of differences in the mass of the elements. Under what conditions would we expect $\Delta\sigma_c$ to be a decreasing or increasing function of the mass of a crystalline system or to be identically zero? Since all the elements have the same mass, any change in σ_c with growth of the crystal would have to derive from changes in the nature of the bonds between elements or in the symmetry pattern. Thus the condition $\Delta\sigma_c \equiv 0$ would hold for any system whose symmetry pattern is invariant with growth. Assuming an inexhaustible supply of elements in the environment and no externally imposed constraints, such systems would continue to grow indefinitely. Simple, inorganic crystals approach this condition and may grow to a relatively large size. However, it should be noted that for such crystals the function

$$\theta_{c,a} = \frac{M_a(\sigma_a - \sigma_c)}{M_c + M_a} - \Delta\sigma_c = \frac{M_a}{M_c + M_a} \cdot k \, ,$$

where k is a constant, decreases monotonically with the mass of the crystal, implying a decreasing affinity of the crystal for a free element and a decreasing rate of growth. Impurities and propagating structural discontinuities, for example, screw dislocations, provide means of circumventing such decline in the rate of growth with increasing size.

Let us consider now crystalline systems composed of much more complex elements, whose characteristic structures may adapt flexibly so as to enable significant variations or modifications in the symmetry pattern. We shall assume that such elements are held together by numerous relatively weak bonds and that the structural flexibility of such systems derives in part from the possibility of altering or rearranging these bonds, while preserving some minimal level of affinities among the elements. Given this possibility, we should expect that σ_c would vary in some way with M_c, that is, $\Delta\sigma_c$ would be a function of the mass of the crystal. It is unlikely that $\Delta\sigma_c$ would be negative for all possible values of M_c since this would imply no upper limit to the possibilities for reordering the bonds between the elements. On the other hand, it would not be surprising if $\Delta\sigma_c$ were negative over some range of growth since this would imply some potential for extending the bonds between elements and increasing the overall stability of such bonds. Thus $\Delta\sigma_c\ (M_c)$, $\sigma_c\ (M_c)$, and the function

$$\theta_{c,a} = \frac{M_a(\sigma_a - \sigma_c(M_c))}{M_c + M_a} - \Delta\sigma_c(M_c)$$

perhaps would have the general forms illustrated in figure 2. Growth of the system would be possible beyond the point of minimum σ_c (where $\Delta\sigma_c[M_c] = 0$) but would cease at the point where $\theta_{c,a}$ approaches zero.

What is the significance of the form of $\sigma_c\,(M_c)$? The decrease in σ_c in the early stages of growth reflects a decrease in the specific entropy s_c of the system, that is, the entropy per unit mass. The increase in σ_c in the later stages of growth corresponds to an increase in s_c. Thus $s_c\,(M_c)$ would have the same general form as that of $\sigma_c\,(M_c)$. Growth beyond the point of minimum σ_c must involve a progressive increase in the specific entropy of the system, and this implies either a uniform in-

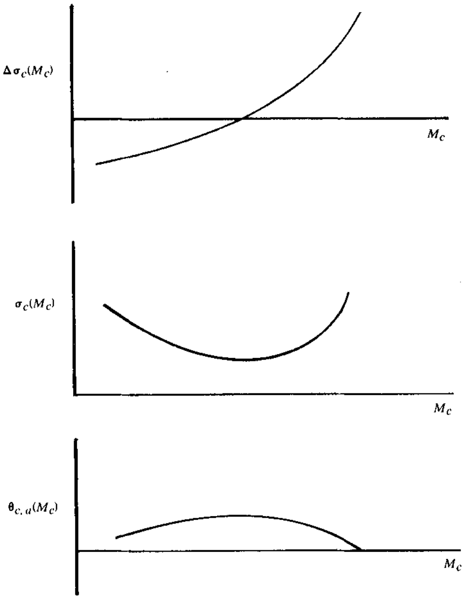

FIG. 2.—General forms of $\Delta\sigma_c$ (M_c), σ_c (M_c), *and* $\theta_{c,a}(M_c)$

crease in the distortion of all bonds in the system, at the one possible extreme, or, at the other, the formation of increasingly distorted and possibly incomplete bonds in localized areas. We may assume that one or the other of these conditions will prevail, depending on the nature and flexibility of the bonds and which of these conditions leads to the lowest specific entropy production. The former condition would give rise to increasing distortion of the basic symmetry pattern, while the latter would generate a new and higher-order symmetry pattern. A transformation of symmetry would be most likely, in view of the growing instability of the system. Growth in the new configuration would proceed either to some more or less stable terminal state or to separation of the system into two or more smaller units. It would appear that microscopic, organic "closed crystals," to use Jacques Monod's expression, are examples of the former case.[16]

EMERGENCE OF SELF-REPRODUCING CRYSTALLINE SYSTEMS

Let us consider the latter course and in particular the possibility that growth might culminate not in some terminal state but in the separation or fissioning of the system into two essentially identical units. This could happen only if the increase in $\Delta\sigma_c$, associated with fissioning, remained well below the thermodynamic limit, that is, $\theta_{c,a}>0$, throughout the fissioning process. (As in the case of simple crystals we would expect the rate of growth to decrease as $\theta_{c,a}$ becomes smaller.) Cleavage would involve a further transformation which would restore the original symmetry pattern in each of the two daughter units. The structural form, specific entropy production, specific entropy and potential for growth of the daughter units would be similar to that of the parent system in its earlier growth phase. Such systems thus would be capable of "self-reproduction." This implies hereditary transmission of information about structure and process from parent to heir.[17] Where and how is this information stored and transmitted in such simple, hypothetical, self-reproducing systems? Since the primary lattice structure and the potential for growth and formation of higher-order symmetry patterns (associated with fissioning) are determined by the characteristic structure of the elements, it would appear that the hereditary information is embodied in the structure of the elements themselves. Thus the elements serve not only as building blocks for the construction of a higher-order, self-reproducing system but also as repositories of specifications describing the processes of construction and self-reproduction of the system. The characteristic structure of the elements serves in effect as an open hereditary program, which specifies how the elements may combine and how and to what limits each may adapt to conditions in the immediate environment, including those imposed by the growth and structural development of the system as a whole.

Such hypothetical, self-reproducing social systems would have in common with simple, ideal crystals a potential for unlimited growth, albeit not as a single structure but through the proliferation of similar units of limited size. It should be noted here that impurities or irregularities of one sort or another play important roles both in the nucleation of real crystals and in determining the manner and limits of growth. Thus, if the nucleation of a crystal is a relatively improbable event and if its growth is subject to constraints arising from impurities or structural irregularities (or the lack thereof), then it would appear that processes which enable continuous growth through self-reproduction and the proliferation of relatively small units would provide a means of circumventing these limitations. The phenomenon of self-reproduction thus may be viewed as a mechanism which facilitates the ordering of elements and thereby the decrease of entropy production and energy dissipation in a closed thermodynamic system. Unlike simpler crystals, self-reproducing crystalline systems would be characterized by undamped oscillation of specific entropy production, specific entropy, and specific energy flux e_c and materials flux ρ_c about minimum values with a period corresponding to the cycle of reproduction, as illustrated in figure 3. As we shall see later, such oscillation of thermodynamic parameters about minimum (or maximum) levels is characteristic of living organisms.

The above arguments presumably would apply also to processes of self-reproduction involving budding of new units from the parent system. The particular mode of self-reproduction for a given system or class of systems apparently would depend on internal structural considerations as well as environmental factors. In either case the arguments suggest that the fundamental distinction between growing social or crystalline systems that are capable of self-reproduction and those that are not has to do with the degree of flexibility of the bonds holding the elements together and therefore with the adaptability or openness of the characteristic structures of the elements. This would appear to be the fundamental prerequisite for the emergence of self-reproducing systems, namely, the creation, via thermodynamic selection processes, of complex "elements" which have highly open and adaptive characteristic structures.

Before proceeding with a more detailed examination of the growth and fissioning process, I should note that while the specific rates of entropy production and energy and materials flux oscillate about minimum levels the total entropy production in and the total flows of energy and materials through the population of self-reproducing systems increase as the population increases. However, since the total number of elements is conserved and since the transfer of an element from the free to the bound state is accompanied by a decrease in the specific entropy production of the element, we see that the total entropy production of the thermodynamic system as a whole decreases toward a minimum, stationary-state value. By the same token, the negentropy and free energy of the steady-state system increase toward maximum values.

Let us now reconsider the growth and fissioning process, which was implicitly assumed to be free of error and disordering forces. We shall assume more realistically that (1) other similar but not identical ele-

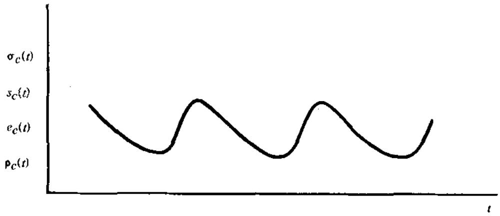

FIG. 3.—General forms of $\sigma_c\ (t)$, $s_c\ (t)$, $e_c\ (t)$, and $\rho_c\ (t)$

ments exist in the environment which have some finite probability of bonding to the system and (2) energetic interactions may lead on occasion to degradation or destruction of the system. The first assumption would permit infrequent mutations in the composition and structure of the self-reproducing systems, which might facilitate or impede the growth and fissioning process, while the second would imply that a system would have only a certain statistical probability (less than unity) of completing the growth and fissioning cycle. Thus under these conditions we might expect some recycling of elements between the free and bound states and competition between mutant forms of self-reproducing systems for available elements in the environment. The principle of thermodynamic selection asserts that that variant form of a class of spontaneously created systems which, other things being equal, has the lowest specific entropy production will have the highest frequency of occurrence in the total population of such systems. We may assume that this applies to all kinds of systems, including self-reproducing systems, if the selection criterion is expressed in terms of the mean value of specific entropy production. Therefore, any mutation which serves to decrease the mean specific entropy production of a self-reproducing system will tend, other things being equal, to increase the probability of continuous growth through the fissioning or self-reproduction process and hence the frequency of occurrence of such mutant forms in the total population. In more familiar terms we would say that natural selection favors mutations which increase the probability of self-reproduction of a species. Evidently, the principle of natural selection is a special case—applying only to self-reproducing systems—of the more general principle of thermodynamic selection. Thus it would appear that the principle of natural selection may be formulated in terms of the laws of thermodynamics in some such manner as stated above. Such a formulation of the principle of natural selection therefore would have the character of a fundamental physical law.

Most importantly, a thermodynamic formulation of the principle of natural selection should enable us to understand better how simple self-reproducing systems evolve into more complex, highly organized systems; how, at the same time, they may come to form symbiotic and social associations with other dissimilar and similar systems; and, finally, how hierarchical systems of higher and higher order come into being. Let us consider these problems in the order listed.

EVOLUTION OF AUTOTROPHIC, SELF-REPRODUCING SYSTEMS

The hypothetical self-reproducing systems which I have been discussing are complete "heterotrophs," that is, all of the constituent elements are obtained from the environment rather than being synthesized within the system. Consequently, their potential for evolving into more complex systems is limited by the availability of elements produced externally. More extensive evolution would be possible only if and to the degree that such systems could acquire a capacity for synthesizing many or all of their structural elements from simpler components in the environment. Such synthesis might be effected either through autocatalysis, that is, self-reproduction of elements within the system, or cyclic catalytic processes in which one class of elements synthesizes elements of another class that in turn facilitate the synthesis of elements of the first class.

If, as has been implicitly assumed, the elements of the hypothetical self-reproducing systems have little or no capability in the free state for autocatalysis, then it would be necessary to conclude that any significant autocatalytic activity would derive from the structural arrangement of the elements in the system. It is necessary to be quite specific on this matter. The evolution of such systems may proceed toward an increasing capacity for internal synthesis of its principal elements and therefore toward increasing organizational complexity only if a viable mutant element has a sufficiently high probability of bringing about the synthesis of a similar element during its lifetime. In other words, the mutant element must be self-reproducing in the conventional sense of the term. This would be possible only if the stability and potential for autocatalytic activity of the element were sufficiently increased by virtue of its incorporation in the larger system. We should expect some such increase in the stability of elements in mutual association and perhaps some enhancement of autocatalytic activity. Indeed, a significant increase in the rate of autocatalytic synthesis of elements might occur under conditions of structural deformation associated with fissioning. Moreover, it is reasonable to suppose that mutant elements might be acquired most readily from the environment or synthesized internally under such conditions. While thermodynamic selection would favor the incorporation of mutant elements which have greater stability and autocatalytic activity in such systems, it would not necessarily lead to a capability for self-reproduction of the elements of a system. All we can say is that if this were to happen then the way would be open for the evolution of increasingly complex self-reproducing systems.

It is important to emphasize that such systems would continue to be social systems in that all of the constituent elements would have similar if not identical characteristic structures. Whether or not such autotrophic systems might come into being in the manner suggested above, they constitute an important class of self-reproducing systems and merit some further attention. Since the structural heterogeneity and organizational complexity of a system generally derive from or are contingent upon differences in the form and function of its constituent elements, we might conclude that systems which synthesize their elements by autocatalysis may not achieve a high degree of organizational complexity. However, this would not be the case if mutations led to elements having increasingly open characteristic structures or hereditary programs, which enable structural adaptation to serve various specialized functions in the system. In effect, the similar elements would become structurally and functionally differentiated in accordance with the developing structural requirements of the system. In more fundamental terms, we would say that the elements would develop differentially and coadapt structurally in such a way as to minimize the specific entropy production of the system at each stage of growth. Thus the general plan of growth, structural development, and self-reproduction of the system would be embodied in the characteristic structure of the elements, and the specific pattern of growth and development would be determined within these constraints by conditions in the local environment. The options for structural adaptation of the elements, including the capability for autocatalysis or self-reproduction, would be subject to thermodynamic constraints imposed at each stage of growth and would be determined in part by the structure of their immediate environment. In this way elements might come to have different forms and functions. Of special interest are those elements which would (1) serve to coordinate the actions of other elements and to govern the overall behavior of the system in its environment and (2) facilitate the reproduction of the system. The need for such elements arises with increasing internal division of labor and capacity for sensing and responding to conditions in the environment, on the one hand, and the progressive loss of totipotency which may accompany the differential development of elements, on the other. These special functions might be combined in a single class of differentially developed elements or be served by two different classes of elements, depending on the nature and complexity of the system.

It will be apparent that the structural integrity and viability of such systems would be contingent on the maintenance of a common characteristic structure among the elements since even relatively infrequent mutations in the synthesis of new elements during the growth process soon might lead to conditions which make the necessary coadaptations of elements impossible. We should expect these difficulties to increase with the evolution of larger and more highly organized systems composed of more complex and open-structured elements. The problem is essentially that of making copies of copies, rather than making multiple copies from a single template. Therefore, we may conclude that highly organized self-reproducing systems of the sort under discussion might evolve only if the mutation rate were sufficiently small. Thus thermodynamic (natural) selection would favor mutations which tend to open the characteristic structure of the elements and at the same time increase both the efficiency and precision of the autocatalytic process. How far such self-reproducing social systems might evolve would depend on the extent to which these various requirements might be satisfied for particular classes of elements and systems and particular environmental conditions.

Let us now consider an alternative approach to the synthesis of complex elements in self-reproducing systems, namely, the possibility that structural distortion associated with fissioning might lead to the synthesis of a new class of elements, perhaps by the attachment of other components to the stressed elements. Such a development could have significant evolutionary consequences if (1) the elements of the new class might serve as templates or catalysts for the synthesis of the structural elements of the system and (2) viable mutant structural elements resulting from such synthesis in turn might synthesize corresponding mutant templates in subsequent fissioning processes. This would be a cyclic catalytic process operating not within a reproductive cycle but between successive reproductive cycles.

In order to make this concept clear, I shall say that the structural and template elements of the system belong to the classes A and α-A, respectively. The hyphenated label is intended to suggest that a template element is formed by the selective addition of components to a structural element and that the resulting structure may be a complex of two different kinds of elements. The cyclic catalytic process then would involve the synthesis of elements of class α-A by and in association with elements of class A, during fissioning, and the subsequent synthesis of elements of class A by elements of class α-A, in the growth of one or both daughter units. If such systems are to synthesize increasingly complex elements, not available in the environment, and thereby to evolve into more highly organized systems, viable mutations must be preserved in the template elements. This fact may be expressed more precisely in the following way. If P_{α_1} is the probability that a viable element of class α_1-A_1 will synthesize a new structural element of class A_1 during its lifetime and P_{A_1} is the probability that the element A_1 will in turn facilitate the synthesis of another element of class α_1-A_1 during its lifetime, then $P_{\alpha_1} P_{A_1}$ must exceed some minimal level necessary to perpetuate the mutation. Any mutation which increases the probability of such cyclic catalytic activity would have, other things being equal, a selective advantage. This follows because such mutations would tend to decrease the mean specific entropy production of the system by enabling the synthesis of more complex elements and their assembly into larger, more highly organized, and more stable systems. The same arguments apply to self-reproducing systems whose elements are synthesized by autocatalysis.

The emergence and evolution of a cyclic catalytic process imply the creation and addition of a new kind of hereditary program to govern the growth and self-reproduction of a system. Whereas the original hereditary program or characteristic structure of the elements specified how the elements would assemble into a crystalline system, the new program, embodied in the structure of a few special elements, would serve to direct the synthesis of the structural elements. Both kinds of programs are required, the latter to produce the structural elements from simpler components in the environment and the former to direct the "self-assembly" of these elements in the system. The program governing the synthesis of the structural elements is of a higher order in that it specifies the characteristic structure and therefore the program for self-assembly of the structural elements.[18] This situation is in sharp contrast to "autocatalytic" systems in which the hereditary program governing the synthesis of the elements serves also to direct their differential development and assembly in the system.

The synthesis of structural elements from one or a relatively few template elements provides a means of circumventing the problem of cumulative mutations, that is, errors resulting from copies of copies, but the templates must be highly stable and immune to mutations which might arise in the repeated synthesis of structural elements. Moreover, if such processes are to lead to the evolution of complex, highly organized systems, the template or higher-order program must become increasingly open to enable the synthesis of either (1) similar structural elements whose characteristic structures permit a wider range of differential development and adaptation, (2) various classes of structural elements to serve diverse structural and functional needs, or (3) two or more classes of elements, some or all of which may be capable of self-reproduction under specific internal environmental conditions. The first of these possibilities would give rise to processes of structural development similar to those involved in "autocatalytic" systems. The second approach would imply the creation either of a set of different template elements ($\alpha_1 - A1$, $\alpha_2 - A_2$, . . . , $\alpha_n - A_n$) or of an elaborated template ($\alpha - A_1, A_2, \ldots, A_n$) capable of selectively synthesizing the various kinds of required elements. In either case some feedback mechanisms and processes would be required to control the rate of synthesis of the different elements in accordance with the developing requirements of the system. The third possibility would lead to "hybrid" systems in which certain classes of elements may be synthesized from a template or, alternatively, by autocatalysis. Here, as in the second approach, some selective feedback control of the rate of synthesis of the elements would be required. Thermodynamic selection would favor mutations which result in hereditary programs that are increasingly open and that enable more efficient and precise control over the synthesis of the elements. In this way relatively simple and homogeneous self-reproducing systems might evolve into more complex, heterogeneous systems of one form or another. At no stage in the evolutionary process would it be necessary to postulate extremely improbable or fortuitous events. Each mutation would be selected and preserved according to its potential for reducing the mean specific entropy production of the system.

Before turning to other matters, I may note here that the rate of synthesis of structural elements in self-reproducing systems, either by autocatalysis or cyclic catalytic processes, must decrease as $\theta_{c,\,a}$ decreases in the final stages of growth and fissioning. In heterotrophic systems the structural elements are acquired from the environment at a progressively lower rate, while in autotrophic systems it is the simpler components utilized in the synthesis of the structural elements that are acquired at a decreasing rate. From this we see that the rate of autocatalytic synthesis or self-reproduction of elements in social systems is dependent on or controlled by the size or mass of the system in accordance with thermodynamic constraints. The effectiveness of such control depends on the social affinities of the elements, that is, on the cohesiveness of the social system in a particular environment.

EVOLUTION OF SYMBIOTIC AND HIGHER-ORDER SELF-REPRODUCING SOCIAL SYSTEMS

Let us now consider the evolution of such systems in a larger perspective. Having stable and well-defined characteristic structures in their own right, self-reproducing systems may be viewed as "elements" capable in some measure of forming symbiotic or social associations with other dissimilar or similar systems. Such higher-order systems would emerge and would be more or less stable to the extent that the individual systems may adapt their characteristic structures mutually so as to decrease their mean specific rates of entropy production. The arguments are the same as before, except that the elements are now relatively complex, self-reproducing systems. Thus self-reproducing systems will be relatively inert or reactive to the degree that their characteristic structures or hereditary programs are closed and inflexible or open and adaptive. Here the openness of the hereditary program refers not merely to the capability of the elements of a system to coadapt internally but to the capacity of the system as a whole to develop and adapt to conditions in its immediate external environment. Self-reproducing systems therefore may be classed according to whether they are relatively (1) unreactive or inert, (2) reactive but asocial, that is, capable of forming symbiotic but not social associations, or (3) reactive and social, that is, capable of establishing stable bonds with other similar as well as dissimilar self-reproducing systems. (The analogy with chemical elements raises the interesting possibility that the characteristic structures of self-reproducing systems might be grouped in a multidimensional periodic table, which reveals similarities in the affinities or behavior of families of such systems representing different hierarchical levels of organization.) Systems belonging to the first class are singular products of evolution in that they have little probability, barring further structural change, of serving as elements in the creation of higher-order systems. By contrast, systems belonging to the second and third classes will have a more or less high probability of evolving in complex symbiotic or sociosymbiotic systems, depending in part on the nature of their environment, that is, on the extent to which thermodynamic selection may favor such associations. Self-reproducing systems of self-reproducing systems may emerge and evolve when the hereditary program of the lower-order systems becomes sufficiently stable and open and environmental conditions favor the creation of such higher-order systems. Indeed, it will be seen that the evolutionary process is open-ended and that thermodynamic selection may come to operate simultaneously on multiple levels of organization and on different time scales.[19]

SUMMARY AND CONCLUSIONS

The aim has been to develop an abstract model, based on the laws of thermodynamics, to account for the origin and evolution of self-reproducing systems and their organization in complexes of increasing hierarchical order. In order to bring it into sharper focus let us summarize the principal features of this model. The arguments have proceeded as follows:

1. We postulate at the outset a closed, thermodynamic system in which relatively simple elements may combine to form larger and more complex entities in such a way as to minimize the entropy pro-

duction of the system, in conformance with our extended formulation of the second law of thermodynamics and the principle of minimum entropy production, implied therein.

2. We say that an "element," "entity," or "system" is any complex (generally composed of simpler components) whose identity or characteristic structure remains essentially unchanged in some time frame and in the course of interactions or associations with other such elements, entities, or systems. The characteristic structure of an element determines its affinity for other similar or dissimilar elements. An element will be said to have a relatively "closed" or "open" characteristic structure and to be relatively inert or reactive to the degree that its structure may adapt to that of other elements and thereby give rise to stable associations which decrease the entropy production of the total system. Such associations involve the exchange or sharing of some structural component or property of the elements and some mutual accommodation of their characteristic structures.

3. From the principle of minimum entropy production and the fact that entropy production is an extensive property of a thermodynamic system, we derive the thermodynamic criterion for the association of one element with another or, more generally, with an existing complex of elements:

$$\theta_{c,a} = \frac{M_a(\sigma_a - \sigma_c)}{M_c + M_a} - \Delta\sigma_c > 0 ,$$

where $\theta_{c,a}$ is a measure of the affinity of a complex of mass M_c and specific entropy production σ_c for a free element of mass M_a and specific entropy production σ_a, and $\Delta\sigma_c$ is the change in specific entropy production of the complex that would result from the addition of the free element. The probability that a particular kind of complex will be formed by the addition of one or another kind of element to an existing system, or alternatively the frequency of occurrence of such a complex in a large population of systems thus formed, will vary directly, other things being equal, with the value of $\theta_{c,a}$ for each kind of complex. When $M_c >> M_a$, this selection criterion reduces to the following: 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 (where $M_c >> M_a$), or alternatively the frequency of occurrence of such a complex in a large population of systems thus formed, will vary inversely, other things being equal, with the value of the specific entropy production of the complex thus formed. We refer to this restricted formulation of the thermodynamic selection criterion as the principle of thermodynamic selection.

4. "Elements" which are highly stable in the free state, that is,

which have relatively low values of specific entropy production, are singular products of the thermodynamic selection process in that their closed structures prevent them from serving as building blocks in the creation of higher-order systems. The characteristic structure of an element will be more or less open to the extent that the bonds holding the components together permit some relative motion or variation of the structural relationships between components. The larger an element (i.e., the greater the number of components), the more flexible the bonds between components; and the less stable it is in the free state, the more open and adaptive will be its characteristic structure. In general, such elements are created by the successive addition of identical or similar components in some repeating structural pattern or sequence, subject to the constraints imposed by the thermodynamic selection process.

5. Identical elements may combine in a repeating spatial pattern to form "crystals" or crystalline systems. If the elements have relatively closed characteristic structures and if σ_c is constant, that is, $\Delta\sigma_c \equiv 0$, the crystal will have a closed characteristic structure and an invariant symmetry pattern. Such simple crystalline systems may grow to an indefinite size, albeit at a decreasing rate, subject only to environmental constraints. If the elements have a relatively open characteristic structure, σ_c may vary with M_c and the crystal may have a relatively open characteristic structure and flexible symmetry pattern. The growth of such systems will involve progressive modification or adaptation of the characteristic structure of the crystal and may lead either to some maximal size or to separation of the system into two or more parts, depending on the way in which σ_c varies with M_c. The former condition will result when, at some stage of growth, $\theta_{c,a} = 0$. The latter possibility will be realized only if the characteristic structure of the crystal (and therefore of the constituent elements) is sufficiently open such that $\theta_{c,a}$ remains positive and never closely approaches zero.

6. Crystalline systems, which continue to grow not as a single unit but through a cyclic process of growth and separation into smaller units that preserves the characteristic structure of the system, are by definition self-reproducing systems. The essential distinction between such systems and others which lack this capability has to do with the relative openness of the characteristic structures of the elements of which they are composed. The information specifying the form and the process of growth and self-reproduction of the system is contained in the characteristic structure of the elements, which therefore serves as a hereditary program for the system. Once elements with sufficiently open characteristic structures or hereditary programs come into being, through processes of thermodynamic selection,

self-reproducing systems will emerge and proliferate as means of further decreasing the entropy production of the total thermodynamic system. The specific entropy production of such self-reproducing systems oscillates about some minimum value, as does the specific entropy.

7. Since the principle of thermodynamic selection applies at every stage of growth of a self-reproducing crystalline system, we may conclude that any mutation which reduces the mean specific entropy production of the system will tend, other things being equal, to increase the probability of continuous growth through the fissioning or self-reproduction process and therefore the frequency of occurrence of such mutant systems. 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.

8. The evolution of all such heterotrophic self-reproducing systems is limited by the availability of mutant elements produced spontaneously in the environment. Further evolution would be possible only to the extent that such self-reproducing systems might acquire a capacity to synthesize their structural elements from simpler components in the environment. Moreover, it would be necessary that the synthesis of such elements be carried out under the direction of a hereditary program and that viable mutations in that program be preserved in the self-reproduction process. These requirements might be satisfied if the structural elements (1) acquired the capacity to reproduce themselves by autocatalysis within the system or (2) could synthesize (probably during fissioning) a new class of template elements which in turn might bring about the synthesis of structural elements in the daughter systems. Thermodynamic selection would favor mutations which would enhance such autocatalytic or cyclic catalytic processes for the synthesis of structural elements since these processes would tend to increase the mean value of $\theta_{c,a}$ and decrease the mean value of σ_c. If the efficiency of either or both of these processes increased in this way to the point where viable mutant elements had a sufficiently high probability of being replicated, then the way would be open for the evolution of increasingly complex self-reproducing systems capable of synthesizing most if not all of their structural elements. Thus it is suggested that the simplest self-reproducing systems are crystalline, social systems which grow and separate into smaller units and that such dynamic systems may acquire a capacity for autocatalytic or cyclic catalytic synthesis of their complex structural elements.

9. There are important distinctions between these two approaches

to the synthesis and evolution of structural elements in self-reproducing systems. Differentiation of the form and function of the elements of a system implies either that the characteristic structure of similar elements may adapt to various structural and functional requirements or that elements having different characteristic structures come to be synthesized. Thus systems whose elements are synthesized by autocatalysis may become more complex and highly organized to the extent that mutations arising in the autocatalytic process may lead to elements with increasingly open characteristic structures. Such systems would continue to evolve as social systems. That is, the characteristic structure of the elements serves as the hereditary program governing the growth and self-reproduction of the system as well as a template for the autocatalytic synthesis of new elements. By contrast, systems whose elements are synthesized by cyclic catalytic processes will evolve through the creation of various classes of elements to serve special functions and accordingly will appear less and less as social systems. In such systems the hereditary program governing the synthesis and assembly of elements and the process of self-reproduction comes to be embodied in the characteristic structure of a relatively small number of nonstructural or template elements. The rate of synthesis of elements, whether by autocatalytic or cyclic catalytic processes, must decrease as $\theta_{c,a}$ decreases in the later phase of growth and fissioning of the system. This means in particular that the rate of self-reproduction of elements in social systems is dependent on or controlled by the size or mass of the system, in accordance with thermodynamic constraints.

10. Having more or less stable and open characteristic structures or hereditary programs, self-reproducing systems will behave as relatively inert or reactive "elements." As such, they may be grouped in one of three broad classifications according to whether they are relatively (1) inert, (2) reactive but asocial, or (3) reactive and social. Self-reproducing systems having suitably open hereditary programs may proliferate and assemble in growing social systems, which may in turn reproduce themselves as a unit if the bonds joining these systems are sufficiently strong and flexible to insure that the $\theta_{c,a}$ function for the higher-order system remains positive at all times.

The abstract model thus developed is open-ended in that it gives rise to self-reproducing "elements" of increasing size and organizational complexity and their "self-assembly" into hierarchical systems of higher and higher order. The fundamental evolutionary process is repeated at successively higher levels as one or another species of systems at each level acquires the requisite attributes to serve as a building block in the creation of a higher-level system. Each new level emerges in the form of simple social systems (composed of essentially undifferentiated elements), which come to reproduce themselves through fissioning or budding and gradually to evolve into more highly organized systems capable of behaving in increasingly complex and adaptive ways in their environment. The basic architectural plan for the construction of the higher-order system is embodied in the open characteristic structure or hereditary program of the lower-order systems. This, it may be noted, implies the existence of a hierarchy of hereditary programs. At each successive level the higher-order system emerges and evolves as a mechanism for increasing the stability and decreasing the mean specific entropy production of the lower-order systems. In this way systems of "stratified stability" are created, the effect of which is to decrease the total entropy production in a closed thermodynamic system to some minimal, stationary-state level. This conclusion is in agreement with Morowitz's view that steady-state energy flow leads to maximum order and minimum energy flow.[20] It is also in agreement with A. J. Lotka's arguments that evolution leads to maximum energy flow through the biosphere by the proliferation of self-reproducing systems since the incorporation of each simple element into a self-reproducing system contributes to a decrease in the total entropy production and energy dissipation.[21] The buildup of free energy and negentropy in such closed, steady-state systems is achieved in many microquantum steps and a relatively few advances in organizational hierarchy. The process is the counterpart of the evolution of an isolated thermodynamic system toward an equilibrium state of zero free energy and maximum entropy.[22]

These arguments lead to the following observations of a philosophical nature:

There is no fundamental mystery in the hierarchy problem. Elements at one level of organizational complexity in a thermodynamic system will combine to form stable elements of higher order if, in chance conjunction, their characteristic structures may coadapt in such a way as to decrease the total entropy production of the system, in conformance with the proposed extended formulation of the second law of thermodynamics. All elements thus are constructed from existing lower-order entities in a process which serves to minimize the entropy production of the thermodynamic system. That is the general "direction" or "goal" of evolution, and that is the fundamental "function" of all elements and systems thus created.

The function of minimizing the entropy production of the thermodynamic system is realized in all elements by the imposition of constraints on the dynamics of the constituent lower-order entities, thereby decreasing their freedom of movement and behavior and their contribution to the entropy production of the total system.[23] The constraints are derived not from the laws which govern the kinetic behavior of the individual entities but from the laws of thermodynamics, which govern their collective behavior and total entropy states. Indeed, the laws of thermodynamics are, by their nature, constraints of a higher order.

According to the theory which has been proposed, both the form and behavior of living systems and the processes by which they have evolved may be explained in terms of fundamental physical laws. It is therefore a reductionist theory. However, this is not to say that the specific form and behavior of such systems may be deduced from a knowledge of their constituent elements alone. We cannot deduce the specific form and behavior of molecules and the processes by which they are formed solely from a knowledge of their atomic constituents; it is necessary in addition to have a detailed understanding of the environment. And so it is with all higher-order systems. With each hierarchical advance both the systems and their environment become more complex, making it progressively more difficult to acquire the necessary information to account for the specific form and behavior of such systems. This practical limitation on our understanding exists quite apart from uncertainties of a statistical nature or associated with physical measurements. If there has been an error in the logic of reductionism, it has been in the failure to give adequate attention to the role of external factors—in particular the thermodynamic properties of the environment—in establishing the constraints at each successive level of organization.

Implications of the Model

My aim now will be to explore briefly some implications of this model and opportunities for testing its empirical and theoretical utility at various levels of organization and evolution of living systems. Basically, it will be argued that primitive life forms, multicellular organisms, organized colonies of social insects and certain higher animals, and successive hierarchical levels of human society all emerged in essentially the same way, that is, as simple, self-reproducing social systems of essentially undifferentiated elements. All such systems may be characterized by a function $\theta_{c,a}$, which is at all times positive and oscillates about some mean value with a period corresponding to the cycle of reproduction of the system. Such systems reproduce by fissioning or budding, as growth beyond the point of maximum $\theta_{c,a}$ leads to increasing instability of bonds in localized areas. In keeping with the fundamental premise of the model the earth is assumed to be a closed thermodynamic system in a quasi-stationary state. That is, it is assumed that (1) over much of the earth's history the energy flow from the sun to the earth has been essentially constant and equal to the energy flow from the earth to outer space and that (2) there has been no significant gain or loss of matter to or from the earth.

Before proceeding to discuss the implications of the model, I should like to comment briefly on recent efforts to account for the phenomena of growth, development, and aging of organisms in terms of the concept of minimum entropy production. Recognizing that all living organisms constitute open thermodynamic systems, Prigogine and J. M. Wiame suggested that growth, development, and aging processes are accompanied by a progressive decrease of specific entropy production, leading to some minimum stationary-state level.[24] Zotin has sought to show that the Prigogine-Wiame theory applies generally to all animal species from the earliest stages of embryological development if the specific rates of entropy production are properly computed.[25] Moreover, he argues that measured increases in the specific heat production associated with the early stages of oogenesis, fertilization, hatching or birth, moulting, wound healing, and carcinogenesis are not in conflict with the Prigogine-Wiame theory since all such processes involve changes in either external or internal parameters which lead to new stationary states. While there remains some doubt concerning the applicability of the Prigogine-Wiame theory to nonlinear processes operating in living systems, the empirical data reviewed by Zotin—especially relating to aging in mature organisms—strongly supports the theory. Since the model which has been proposed here is based on a further generalization of the principle of minimum entropy production, it would appear that these data provide broad support also of the model.

ORIGIN OF LIFE AND EVOLUTION OF UNICELLULAR ORGANISMS

The proposed model offers a way around the perplexing problems having to do with the synthesis of proteins, specific enzymes, and nucleic acid templates in the first self-reproducing systems.[26] As essentially complete heterotrophs such systems had no need to synthesize elements. Self-reproduction was a relatively simple matter of the "self-assembly" of organic macromolecules (produced spontaneously in the environment) into crystalline structures, whose growth culminated in their separation into similar, smaller units. The capability for synthesizing such structural elements and the more complex molecules which serve to direct and carry out such synthesis gradually evolved from this beginning.

There is significant evidence to support this view of the origin of life in experiments undertaken by S. W. Fox and his associates.[27] These researchers have shown that thermally produced amino acids may combine without direction of nucleic acids to form systematic sequences of amino acid residues. Such "proteinoids" exhibit weak, broadly specific catalytic properties and are capable of readily combining in spheroidal, crystalline systems, which grow in size and multiply by a process of binary fission or budding. Moreover, such systems evidence a capacity to metabolize, to undergo selection, to bind to polynucleotides, and to associate in clusters. As Fox has observed, they appear to grow and replicate as nearly complete heterotrophs. The possibility that life commenced in this way has found further support in the discovery of microsphere inclusions in quartz crystals from the Precambrian of Southwest Africa, which are similar to the microspheres produced in the laboratory.[28]

If accurate measurements could be made of the rate of growth (and perhaps of entropy production) of proteinoid microspheres at various stages of the reproductive cycle and under various controlled environmental conditions, it might be possible to test, at least indirectly, the validity of the model. It would be of particular interest to determine whether, to what extent, and in what phase of the growth and fissioning cycle the autocatalysis of proteinoids is enhanced in microspheres. Similarly, it would be desirable to determine at what phase of the growth and fissioning cycle and in what regions of the microspheres the binding of polynucleotides is most pronounced. And finally, if it were possible to make accurate measurements of the mean specific entropy production of such systems, we might put to a direct test the principle of thermodynamic selection by conducting systematic evolutionary experiments under controlled laboratory conditions. In this regard it would be highly significant if it could be demonstrated that thermodynamic selection leads to a progressive increase in the internal synthesis of proteinoids, either through autocatalysis or cyclic catalytic processes involving polynucleotides. Since there are no existing cells composed of similar self-reproducing elements, we must conclude either that the capacity for autocatalytic synthesis of structural elements never evolved to a sufficient degree or that such systems were at a selective disadvantage in competition with systems which evolved through cyclic catalytic processes.

According to the model, all of the complex apparatus involved in photosynthesis, respiration, protein synthesis, mechanical propulsion, the sensing of changes in the external environment and the homeostatic control of the internal chemical state, the ingestion of nutrients and discharge of wastes, and the preservation, transmission, exchange, and recombination of genetic materials evolved by the thermodynamic selection of mutant systems, having progressively lower values of mean specific entropy production and capable of reproducing in diverse and changing environments. As various species of primitive cells became more complex and highly organized and their hereditary programs more open, they formed symbiotic and social associations, thereby effecting a further decrease in their mean specific rates of entropy production.[29] It would appear that the nuclear organization of genetic materials in the eukaryotes evolved, coincident with the increase in organizational complexity, as a hierarchical control system to govern the growth, development, and reproduction of the cell and to enable the cell to adapt its form and behavior to conditions in the social and natural environments. Thus we should expect measurements of the mean specific entropy production of various species of unicellular organisms to be correlated to their organizational and behavioral complexity and to the extent to which they are capable of forming colonial associations. In particular we should expect that the eukaryotes would have significantly lower levels of mean specific entropy production than prokaryotic cells.

ORIGIN AND EVOLUTION OF MULTICELLULAR ORGANISMS

It would appear, as has been frequently argued, that multicellular organisms evolved from one or more species of protozoa.[30] According to the model, the first multicellular organisms emerged as close-knit colonies of essentially undifferentiated cells which grew in population and fissioned or budded off to form similar new colonies. The fundamental criterion is that the function $\theta_{c,a}(M_c)$, characterizing the affinity of the colony for each newly produced cell, remains sufficiently positive, as growth leads to the fissioning or budding of the colony into two or more units. If this interpretation is correct, then all colonial systems of protozoa, which are capable of growth and fissioning or budding and thereby generating new colonies, are in fact simple, self-reproducing multicellular organisms. Thus the problem of the origin of multicellular organisms would appear to center principally on the task of tracing the evolutionary course from such simple colonial systems, which reproduce by fissioning or budding, to the more complex organisms in which reproduction is carried out by specialized subsystems. In this respect the problem is similar to that of accounting for the origin of present-day cells.

It should be possible to test the validity of these ideas experimentally, possibly by direct comparative measurements of the levels and rates of change of specific entropy production of various protozoan colonial systems. Moreover, it should be possible to identify and describe quantitatively the "components" which are exchanged or shared among the individual cells in the formation of social bonds and to determine the form and extent of mutual structural accommodation or coadaptation thus imposed.[31] And finally at this level it might be possible to test directly the validity of the principle of thermodynamic selection by measuring and comparing the mean specific rates of entropy production of mutant strains of cells and colonial systems of cells under carefully controlled laboratory conditions. That is, it might be possible to identify factors in the environment which favor a colonial form of existence and in controlled experiments to isolate mutant strains which have a greater or less potential for forming self-reproducing colonial systems. According to the principle of thermodynamic selection those strains which exhibit a greater potential for establishing such colonies will have a lower mean specific entropy production.

From such simple beginnings multicellular organisms evolved into more tightly knit and highly organized self-reproducing social systems of self-reproducing cells. As the genetic program of the cells became more open, their capacity to adapt in form and function increased, giving rise to specialization, division of labor, and the formation of various organs and tissues. The role which each cell came to play in the organism was determined by constraints imposed by the immediate environment in which it emerged, that is, by systemic control of the expression of genetic information in each cell. The increase of organizational complexity led in particular to the evolution of two subsystems of special interest. The function of the one was to facilitate the reproduction of the organism as a whole. Thus certain cells develop as reproduction specialists or, expressed differently, as totipotent generalists to bring about the production of a new organism. The adaptive development of such cells is equivalent, at the lower level, to the replication of the genetic template. The function of the other subsystem was to coordinate and regulate the behavior of the various organs and to enable the organism as a whole to respond and adapt to conditions in the environment. This subsystem gradually evolved into the endocrine and neural control systems. The capacity of multicellular organisms to adapt morphologically and behaviorally to conditions in their environment and therefore to establish symbiotic and in particular social associations was determined by the extent to which these control systems became open and responsive to changes in the external as well as internal environment. These control systems have evolved thus to serve as more or less open hereditary programs, governing the nature and extent of adaptation of organisms to their environment and in particular the formation of symbiotic and social associations.

The evolution and speciation of more complex multicellular organisms proceeded, as before, by the thermodynamic selection of mutant systems, having lower mean specific rates of entropy production and capable of reproducing in various environmental niches. Speciation occurred as thermodynamic selection led to mutant strains of organisms whose mean specific rates of entropy production were minimal under different environmental conditions. As the structural and/or behavioral characteristics of the different strains became increasingly differentiated, the possibility of viable sexual exchange and recombination of genetic materials decreased. Depending on the nature of the environment, thermodynamic selection gave rise to more or less closed or open genetic programs in the different species. While most if not virtually all species were capable of forming symbiotic associations, it would appear that only a relatively few were able to establish extensive social associations. All such associations, whatever their nature and extent, served to decrease the mean specific entropy production of the participating organisms and therefore may have played a more or less significant role in the speciation process. This view represents an extension of the argument that ethological barriers to random mating constitute the largest and most important class of isolating mechanisms in animals.[32] It may be noted here that parasitic associations would be expected to lead to a decrease in the mean specific entropy production of one organism at the expense of an increase in that of the other.

These conjectures should be susceptible to empirical test at various phylogenetic levels. Thus, for example, it should be possible to measure and compare the mean specific rates of entropy production of closely related species and determine whether they correlate to differences in the extent and nature of their social behavior. Moreover, it might be possible with certain species to determine whether, as the model predicts, the specific entropy production of a colony commences to increase at some stage of growth of the colony, thereby leading to a decrease in the growth rate. If so, we might reasonably conclude that control of the populations of social organisms may be explained in terms of fundamental thermodynamic laws. Also, it might be possible to conduct experiments to determine whether the social order of a species contributes to a decrease of the mean specific entropy production of the individuals. This perhaps could be ascertained by comparative measurements on groups of individuals raised under normal conditions and under conditions which are otherwise similar but inhibit the formation of social bonds.

ORIGIN AND EVOLUTION OF SELF-REPRODUCING SOCIAL SYSTEMS OF MULTICELLULAR ORGANISMS

From Darwin's time to the present the social insects have presented a special challenge to those concerned with evolutionary theory.[33] The problem has been to account for the origin and quasi-organismic character of insect colonies as manifested not only in their extraordinary organizational and behavioral complexity but in the manner in which the colonies as a whole are reproduced. This problem comes into sharper focus in the light of the proposed model. Indeed, we see that the insect colonies are unique among the social systems of multicellular organisms only in the extent and rigidity of their organizational arrangements and in the mechanisms and processes which govern the development, behavior, and reproduction of such systems. According to the model the insect colonies emerged as increasingly stable and extensive aggregates of essentially undifferentiated individuals, which came to reproduce as a unit through processes of fissioning or budding. As the genetic program became more open and the capacity for morphological and behavioral adaptation increased, various specialist roles emerged, giving rise to increasing division of labor in the colony. Each viable mutation in this process led to a decrease of the mean specific entropy production of the individuals and of the colony as a whole, as illustrated in figure 4. With only rudimentary nervous systems, their functional differentiation was achieved largely through differences in morphological development, associated either with the age or sex of the individual or induced by chemical or other signals in the social and natural environment. Thus the endocrine control system evolved to serve as an open hereditary program governing the morphological development and behavior of individuals in accordance with constraints imposed by the colony at various stages of its growth and development. The social bonds were implemented by such morphological adaptation, by the exchange or sharing of nest sites, food materials, and glandular secretions, and by tactile and other sensory means of communication. In the course of evolution, increasing organizational complexity in the colony was accompanied by increasing systemic control of the rate of self-reproduction of the individual organisms. In certain species, as in the case of the social bees, the "elements" or individual members of the colony came to be "synthesized" or produced from a single "template" in a quasi-cyclic catalytic process. In such species one or a relatively few reproductive queens produce large numbers of fertilized eggs. The eggs and larvae are cared for by an earlier generation of workers. The new generation of workers that emerge in this way produces a limited number of unfertilized eggs which develop into males, whose sole function is to inseminate the queen. The colony is reproduced when one or another of the larvae is nourished to sexual maturity and leaves the parent hive or nest to mate with a male and establish a new colony. The processes of growth, development, and reproduction of such colonies are similar in many ways to those operating within the cell.

There would appear to be numerous opportunities to test the pro-

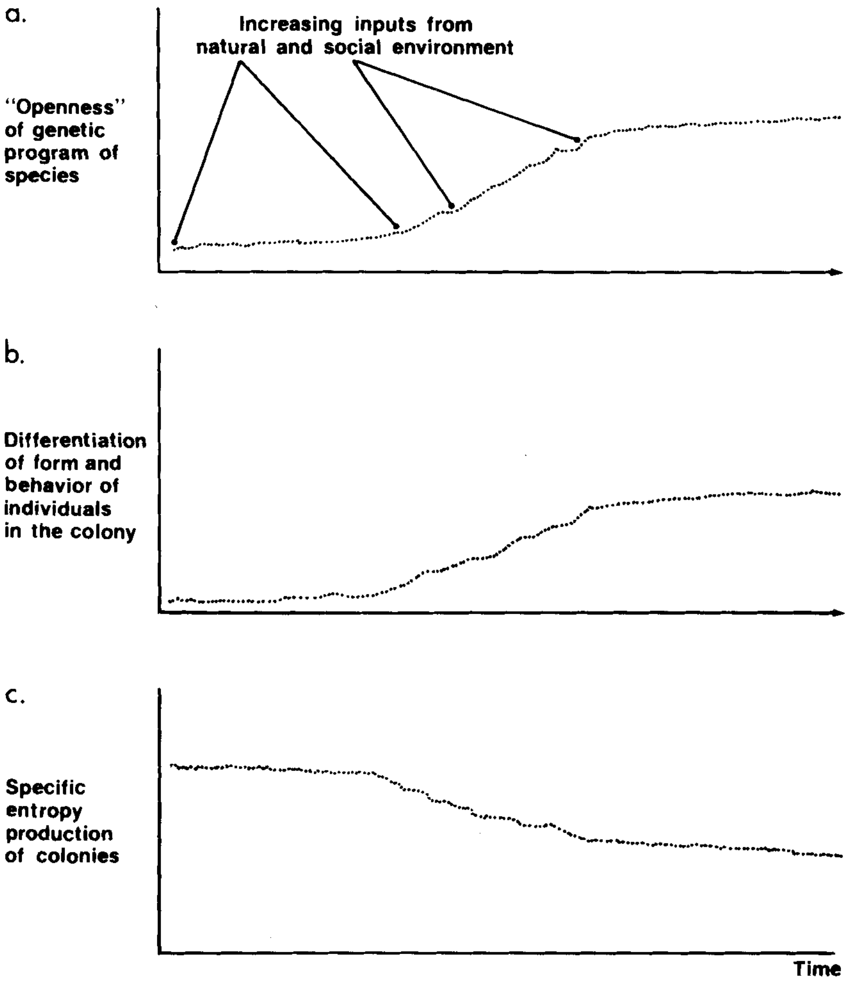

FIG. 4.—Evolution of social systems of insects resulting from increasing "openness" of genetic expressivity to factors in the natural and social environment (*a*) and characterized by increasing differentiation of individual form and behavior (*b*) and decreasing specific entropy production of colonies of the species (*c*).

posed model by comparative measurements of the entropy production parameters of various species of insects and insect colonies. It may be sufficient here to note that the collectively constructed nests and other artifacts of such colonies very likely play an important role in minimizing the mean specific entropy production of the individuals and of the colony and therefore may merit special attention in such experimental studies. Similarly, we might expect that symbiotic associations between different species of social insects would be important in minimizing the mean specific entropy production of the colonies.

In higher animal species the potential for chemically mediated morphological adaptation became increasingly limited, while the potential for behavioral adaptation gradually increased with the evolution of the central nervous system (CNS). The result was an apparent retrogression in the evolution of animal social systems. In many species social behavior was largely associated with courtship and mating and was genetically "wired in," that is, not acquired through learning. That is to say, the nervous system and associated sensory and motor control systems evolved in such a way as to serve a limited number of specific behavioral needs. At higher phylogenetic levels the genetic program governing the development of the CNS became increasingly open to control of expressivity by factors in the external as well as internal environment of the organism. The evolutionary process was similar to that characterizing the evolution of social insects, as depicted in figure 4, except that the differentiation and integration of the behavior of individuals were effected increasingly through the adaptive development of the CNS rather than by way of morphological development. The implication here is that the structure of the CNS of higher animals develops to a greater or lesser extent over the life of the organism, in adaptive response to such factors. If this is so, then learning or adaptive behavior involves control, by external as well as internal factors, of the expression of genetic information in the cells of the CNS and associated neurosensory and neuromuscular apparatus. Arguments relevant to this idea are presented by R. Mark, K. H. Pribram, B. F. Skinner, and John R. Platt.[34] Indeed, it would appear that learning involves thermodynamic selection of alternative structural possibilities of the CNS such that the resulting patterns of behavior will enable the organism to maintain a minimum specific entropy production at each stage of growth and development. The same holds for the collective learning of a social group. The potential for behavioral adaptation in this way is far greater than may be realized by the more limited modes of morphological and behavioral adaptation utilized by the insects and other lower life forms.

Thus the CNS evolved in the various species as a more or less open, adaptive structure or program which, to the limits of its potential, enabled the formation of more or less extensive, highly organized, and flexibly structured social systems. That is, the capability for growth, development, and self-reproduction of the social system was determined by the adaptive potential of the CNS in essentially the same way that the capacity for establishing self-reproducing colonies of cells was determined by the openness of the genetic program of the various species of protozoa. How the characteristic structure of the CNS was adapted in each organism, and therefore how the organism behaved and functioned in the social unit, was determined in part by constraints imposed by the social system. From this it may be concluded that the CNS has come to function in the higher species as a hereditary mechanism, determining the structure and functioning of the social system and acting as an agent to preserve and transmit information about the system. Needless to say, the processes by which such hereditary information are replicated and transmitted from one generation to the next within the social unit or from a parent social system to a daughter unit differ greatly from those involved in genetic mechanisms.[35] So also do the mechanisms and dynamics of mutation and selection differ radically. Nevertheless, the process of thermodynamic selection operates in the same fundamental way on all organized systems. The specific form and behavior of such social systems are determined in part by the environment; that is, the system evolves in such a way as to achieve a minimum level of mean specific entropy production in a particular environment. Thus the social systems of a species might vary considerably in size and form under different environmental conditions. Indeed, it would appear that the territorial behavior of animal societies may be accounted for ultimately in terms of the concept and process of thermodynamic selection. In effect such social systems become speciated, and to the extent that this is so we should expect to find increasingly fierce competition and conflict between different social groups of the same species. These arguments would appear to have special significance for the study of competition and conflict between human social systems.

According to the model, the size or population of animal societies should grow, beyond some level, at a decreasing rate either to some maximum level at which the function $\theta_{c,a}$ approaches zero or, if the hereditary program is sufficiently open and adaptive, to a point where the social system fissions or buds off to form a new unit. This assumes of course an adequate supply of resources in the environment and the absence of predatory or other constraints on growth. Moreover, evolution of the social systems of animals should lead to some division of labor and in particular to the emergence of hierarchical controls governing the behavior of the individuals and their capacity for or rate of self-reproduction. The dominance hierarchies and harems which are characteristic of the social systems of many higher species would appear thus to have evolved through processes of thermodynamic selection as ways of decreasing the mean specific entropy production of the group and its members.

HIERARCHICAL EVOLUTION OF HUMAN SOCIAL SYSTEMS

The proposed model leads us to believe that social systems of hominids and the early tribal societies of humankind evolved similarly through processes of thermodynamic selection, albeit with highly distinctive features. Our concern here will not be to speculate on the course of such evolution but to try to understand the more recent course of human social evolution, which has given rise to the creation of hierarchical systems of still higher order. Clearly, the evolution of the brain and other physiological attributes which distinguish *Homo sapiens* from their primate ancestors was essential to the formation of such social systems of social systems since no other species of multicellular organisms has accomplished that feat. For all their remarkable behavior, we find no colonies of colonies of social insects. This is not surprising since the characteristic structure of insect colonies is relatively rigid and closed, providing little opportunity for structural coadaptation of similar colonies so as to decrease their mean specific rates of entropy production. The same may be said of the social systems of higher animals. As was earlier noted, social systems may become structurally and behaviorally adapted to conditions in their immediate environment, leading them to defend their territories against encroachment by other social groups of the same species. For such systems to combine in the formation of a higher social order it would be necessary that each social group achieve some reduction of its mean specific entropy production through the exchange or sharing of resources or produced "goods and services," and this in general requires some coadaptation of the structure and behavior of each system.

Such cooperative interaction among early human tribal societies gradually emerged as they proliferated through processes of fissioning or budding and evolved into more highly organized and open-structured systems. This is not to say that intertribal competition, conflict, and defense of territory ceased, as the subsequent history of civilization attests. These developments were both the result and the cause of further opening of the genetic program and the characteristic structure of the CNS.[36] The increasing structural and behavioral complexity of the tribal societies was accompanied by the evolution of language, communications, traditions, ceremonial practices, laws, and governmental systems which served to control and coordinate the behavior of individuals and thereby to define and preserve, from generation to generation, the characteristic structure or hereditary program of the society. When such hereditary programs became sufficiently open and adaptive, it became possible for the tribal societies to combine and establish larger and more permanent settlements, from which the city-states evolved. This process was in turn accompanied and facilitated by various social, cultural, technological, economic, and governmental advances, about which a great deal has been written.

It would appear that the ancient empires emerged and evolved in essentially the same way, as the characteristic structures or hereditary programs of the proliferating city-states became sufficiently open to enable them to combine and establish integral social, economic, and governmental systems of still higher order. Again, this is not to ignore the role played by competition, conflict, conquest, and the institution of slavery in the creation of such empires. Indeed, the model would suggest that the capacity for exchange or sharing of natural resources, goods and services, cultural ways, and defense systems over extensive geographical areas was insufficient to maintain indefinitely the attachments that were so often formed through conquest. The breakup of the ancient empires, the retreat into the Dark Ages, and the emergence of nation states from feudal societies may be seen as the termination of one evolutionary experiment in the self-organization of communities and cities into larger systems and the start of another. Whether nation states in their present forms will prove to be viable organizational units in the evolution of human society remains to be determined. The test, as at all lower levels of sociobiological evolution, has to do first with the extent to which such organizational systems enable the lower-order entities to achieve a minimum mean specific entropy production and second with the possibility that the higher-order systems themselves may serve as elements in the formation of a larger complex, thereby further reducing the mean specific rates of entropy production of the lower-order entities.

Perhaps we could determine the soundness of this reasoning about the evolution of human society by comparing estimates of the levels and rates of change of mean specific entropy production of the various social systems derived from archaeological, anthropological, historical, and contemporary socioeconomic data. We should expect that significant changes or differences in these parameters would be correlated with organizational and technological advances. The latter prospect raises the intriguing notion that the technological artifacts of human society have evolved, by and large, as instruments for reducing the mean specific entropy production of the social systems. This would appear to be at odds with the historical increase in per capita energy use. The apparent conflict vanishes when we realize that all such artifacts are in fact ordered elements of the social system and their mass and specific entropy production must be taken into account in estimating the specific entropy production of the total system. The fact that they are composed of inanimate matter is of no consequence in the thermodynamic analysis. This necessarily complicates the task of estimating the specific entropy production of human social systems, but it enables us at the same time to understand better the fundamental nature of such systems.

Thus the proposed model suggests that the structure of human society, no less than the structure of cells, multicellular organisms, and animal societies, has been shaped by fundamental processes of thermodynamic selection, as illustrated in figure 5. This view appears

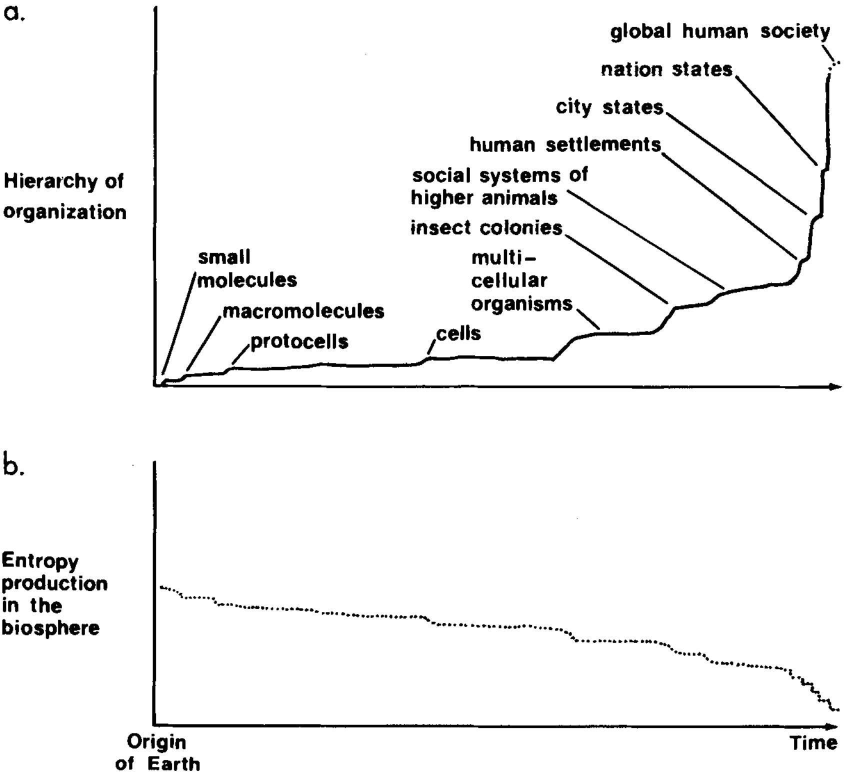

FIG. 5.—The origin and hierarchical ascent of living systems (*a*) and the accompanying decline of entropy production in the biosphere (*b*).

at first glance to be disturbingly mechanistic, deterministic, and devoid of all consideration of the human spirit. In fact, it would appear that the diverse cultures and achievements in art, literature, education, science, technology, industry, and government, which are unique to humankind, could be only the result of some fundamental ordering process. Indeed, it is our awareness of the spatial and temporal patterns of order and differences in these patterns that causes us to marvel at the workings of nature and the accomplishments of human beings. The possibility that a species of life might come to understand, if only in a general way, the processes by which all such ordered systems come into being and evolve should lead us to an even more profound sense of wonder and respect for the workings of nature. However, there is a more important and urgent reason for the pursuit of such knowledge. We are in the process of establishing a global human society with enormous potential for influencing or controlling the further evolution of all life on earth. There is growing concern that the ignorant exercise of such power may do irreparable harm to the biosphere. Evolution is making us trustees of the biosphere, which means that we must learn how to anticipate the long-range consequences of our actions and to manage our further social development wisely.

The proposed theory of the origin and hierarchical evolution of living systems, if substantially sound, would provide perhaps a more fundamental foundation for the development of the social sciences and, it is hoped, a more effective approach in dealing with contemporary problems and avoiding or minimizing problems in the future. While we cannot predict the precise course of evolutionary systems, for reasons presented earlier, it should be possible to assess the viability of alternative policies and paths of social development in terms of the fundamental constraints imposed by nature. It would appear that the principles of minimum entropy production and thermodynamic selection would have particular relevance, for example, to the analysis of problems and the formulation of policies having to do with the use of energy and materials, environmental pollution, food production, population control, transportation, urban congestion, arms control, and technological development. Such global problems and many others of a more subtle nature are perhaps manifestations of a more fundamental problem, namely, the deviation of human social evolution from the path of minimum specific entropy production and energy dissipation.

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