

EVOLUTION TOWARDS INCREASING ENTROPY  
ACCORDING TO THE BOLTZMANN MODEL

Jerry C. Jordan, Jr.\*\*  
4454 Morse Ave.  
North Hollywood, CA 91604

Received 6 November 1990; 20 June 1990

**ABSTRACT:** The Boltzmann model of the microstructure of systems is employed to test whether organic evolution is towards increasing entropy. The long-term trends of evolution are compared to eight widely recognized criteria of increasing entropy. Brillouin's concept, that information represents negative entropy, is extended, and equations are developed in order to demonstrate that information theory is an extension of thermodynamic theory. In this context, evolution is shown to generate information as well as entropy. Arguments are presented which indicate that life is far-evolved from the low-entropy, high-information, crystalline structure of the earth's crust. The opinion is expressed that selection produces information, and therefore cladogenesis, which is one manifestation of selection, produces information not entropy. What, then, is the source of the increasing entropy in evolution? Here the entropy is attributed to the energization of life, including the energization resulting in mutation, and the energization which occurs in a variety of common life processes.

\* \* \*

Brooks and Wiley (1984, 1985 and 1988; also Wiley and Brooks, 1982) put forth the thesis that evolution is towards increasing entropy, rather than towards increasing order, as in the past generally has been believed. To develop their thesis, Brooks and Wiley formulated a thermodynamic model which differed substantially from traditional thermodynamic theory. With the first appearance of their thesis, several authors were highly critical (Løvtrup, 1983; Bookstein, 1983; and Wicken, 1983), the principal objections being to Brooks and Wiley's unorthodox interpretations of thermodynamic theory and information theory.

I agree entirely with the Brooks-Wiley dictum that evolution is towards increasing entropy. However, I also have to agree with their critics, that the Brooks-Wiley thermodynamic model is inadequate for demonstrating the thesis. Consequently, this paper will test the Brooks-Wiley increasing-entropy thesis by employing the Boltzmann thermodynamic model.

Four operations will be carried out:

1. The Boltzmann thermodynamic model will be used to define the thesis and also will be used to test it.
2. Brillouin's (1962) interpretation of Shannon's (Shannon and Weaver, 1949) concept of information will be employed and extended,

\* \* \*

\*\*This article is dedicated to Joseph B. Birdsall, Emeritus Professor, Department of Anthropology, University of California, Los Angeles.

Evolutionary Theory 9: 255-277 (June, 1990)

The editors thank D. McShea, R.E. Ulanowicz, and another referee for help in evaluating this paper.

© 1990, Department of Ecology and Evolution, The University of Chicago

making it possible to demonstrate that evolution generates information as well as entropy.

3. Long-term evolutionary trends, which are based upon interpretations of the existing body of empirical evidence from fossils and living organisms, will be presented in thermodynamically-meaningful terms, and will be tested by macroscopic criteria which are in keeping with the Boltzmann model.

4. There will be a thermodynamic reexamination of the entropic implications of speciation, cohesion and energy, as these concepts were discussed by Brooks and Wiley.

The matter of testing the Brooks-Wiley thesis against the material evidence of evolution is of great importance. The Brooks-Wiley thesis has been an issue since 1982, and yet it never has been put to valid empirical test. Brooks and Wiley devoted their energy almost exclusively to abstract theoretical arguments and to hypothetical test models. The small amount of empirical evidence which was used by Brooks and Wiley was directed overwhelmingly at other theses in their general theory.

The problem is not that there is a dearth of evidence on the issue. For more than one hundred years scholars in the biological sciences have studied life in an evolutionary framework. There is an enormous amount of evidence from fossils and from living organisms which can be used to shed light on the question of evolutionary trends. That evidence then can be evaluated according to the formal and traditional concepts of Boltzmann thermodynamics. The difficulty in applying the test to the Brooks-Wiley thesis comes from problems connected with recognizing the appropriate macroscopic criteria for the purpose.

One objective to a thermodynamic study of evolution is to introduce physical principles to the biological sciences. Success in achieving this objective depends upon one's observing certain conventions when defining and measuring entropy. In these matters, as in others, Brooks and Wiley chose an independent course. Since I choose to follow a more conventional course, my conclusions often are at variance with claims made by Brooks and Wiley.

#### BOLTZMANN'S MEASURE OF ENTROPY

Boltzmann developed the conceptualization and mathematical expression of entropy, as it pertains to the microscopic and chemical structure of a system. A methodology for comparing the entropy of life during different stages of evolution can be obtained by applying the Boltzmann model.

Strictly speaking, Boltzmann's equilibrium equations describe isolated systems which already have reached maximum entropy. There are no truly isolated systems in nature, so whenever Boltzmann's equations are applied, a discrepancy always arises between his mathematical model and the real system. Nevertheless, Boltzmann's model is a powerful tool for understanding the thermodynamics of real systems.

For Boltzmann's equation to fit a system precisely, that system must have a fixed amount of internal energy. This energy will change in distribution among the atoms and molecules of the system, expressing itself as various types of movement and excitation of the particles. Each particular distribution of particles among the different levels of energization is known as an energy distribution. An energy distribution is characterized by the different energy levels that are represented among the particles, and by the number of particles at each such energy level. The distance between energy levels is the magnitude of difference in

energization of particles at two different levels of energization.

When applying thermodynamic theory to grossly open systems, such as to living organisms, one must contend with on-going transitions between energy distributions in such systems, and also with changes in the internal energy,  $E$ , and in the material bases of the systems. These last two features result in a whole new set of energy distributions. It is these two attributes of grossly open systems which usually fuel criticism of the use of thermodynamic theory in the study of living organisms. Nevertheless, for any given  $E$ , or for any series of values of  $E$ , and for any given material bases, all with known structural qualities, there is an entropy, and Brooks and Wiley are justified in asking whether this entropy has increased for life in its evolution. Some of the important entropy-affecting physical properties of a system will be discussed presently.

A system with internal energy  $E$  will have a most probable energy distribution. However, it also will assume additional, less common, energy distributions, as the internal energy comes to be divided among the particles in different patterns. Hence, for Brooks and Wiley to have proven that evolution is towards increased entropy, they needed to identify the macroscopic factors which contribute to an increased number of energy distributions and needed to locate these factors in present-day and past life.

Boltzmann found that entropy of a system is the logarithm to the base  $e$  of the number of microstates in the most probable energy distribution of the system.

$$S = K \ln W_{\max}$$

where  $K$  is Boltzmann's constant,  $\ln$  is the natural logarithm, and  $W_{\max}$  is the number of microstates in the most probable energy distribution. Systems with greater entropy have not only a greater number of energy levels, but also have more closely-spaced energy levels, a greater number of energy distributions, and more microstates per energy distribution. The concept of entropy applies not only to the evolution of a single system, but also applies in a comparison of two systems, even if conditions are achieved by changes in  $E$  and by changes in the material bases of the systems.

Any material system has thermodynamic properties and can be studied as a thermodynamic system. Thus, distinctions between thermodynamic systems and nonthermodynamic systems are contrived. Systems which can be studied thermodynamically include nucleotides, DNA molecules, cells, organisms and entire species or entire ecosystems. They also include communication systems, such as signal light systems and radio transmissions, or just print on the page of a newspaper. However, since open systems readily and substantially change in  $E$ , and sometimes entirely change in their material bases, the existing mathematical models of classical thermodynamic theory represent severe simplifications of the system, even if those mathematical models are germane in the fundamental concepts. Fortunately, as will be shown below, information theory provides much of the basis for an open-system thermodynamics.

Mathematical determinations of the total entropy of a system seldom are made. The task is too laborious. Most determinations which are made measure only changes in entropy, and even more commonly thermodynamic theory is used solely to organize one's thinking about the behavior of systems, without any calculations being made. This is possible because the conditions which contribute to entropy are well known.

Because of the concepts of microstate and macrostate which Brooks and Wiley chose to adopt, nowhere in the discourses of Brooks and Wiley was there any indication that early life and present-day life might be

compared in number of energy levels, in the spacing of energy levels, in Boltzmann microstates, in energy distributions, and in internal energy; nor was there the suggestion that early life and present-day life display other measurable qualities which would permit a comparison in terms of the Boltzmann model. These omissions by Brooks and Wiley stem from the shortcomings of their thermodynamic model, not from the obvious technical problems in measuring these quantities.

#### BROOKS-WILEY MODELS OF THERMODYNAMICS AND INFORMATION

By their own description, Brooks and Wiley employed unorthodox concepts of entropy and information. This was in keeping with their independent style, but may have disenchanted some scientists who otherwise would have found their main thesis attractive. It is my belief that Brooks and Wiley encumbered their presentation and made empirical testing more difficult by their choice of undeveloped models of thermodynamics and information theory.

In the Brooks-Wiley presentation, a microstate was any condition of a part of a system which could be distinguished from the conditions of one or more other parts of the same system (Brooks and Wiley, 1988: 36-41). This representation was at variance with the Boltzmann concept, because a Boltzmann microstate embraces simultaneously all of the particles of all of the system.

A Brooks-Wiley microstate could and would be characterized by more than one Boltzmann microstate at any one time. In the Brooks-Wiley model, a system was of thermodynamic interest only if it displayed two or more of their microstates simultaneously, a condition which would prevail only if the system had access to a very large number of microstates in the Boltzmann sense.

From these observations it follows that a Brooks-Wiley microstate did not conform to the Boltzmann formulation of the microstructure of a system. In fact, Brooks-Wiley thermodynamics ignored the microstructure of systems entirely. Microstates were identified by their macroscopic configurations. These characteristics of the Brooks-Wiley model can be illustrated by one of their examples (Brooks and Wiley, 1988: 37).

Consider a very simple case, a one locus-two allele system. The phase space may be defined as the number of possible genotypes. Each genotype class is a microstate. The population (of  $N$  organisms) comprises the system. The macrostate is the distribution of these individuals over the microstates available to the population. The entropy is a measure of this distribution and can be measured directly by

$$H = -\sum P_i \log_2 P_i$$

Where  $P_i$  is the probability of a randomly chosen organism occupying a particular genotype...The result is a measure of the configurational complexity of the population in terms of the distribution of individuals over microstates available to a particular system at a particular hierarchical level of information (in this case, the level represented by genotypes.)

The equation used here by Brooks and Wiley as a measure of entropy is the famous Shannon equation for the "entropy" of a code (Shannon and Weaver, 1949). From this example we learn that a microstate (genotypic class) represented only part of the system (population) so that the system might be composed of more than one microstate at any one moment. Since the system was comprised of one particular locus, as found in all

the members of a population, a single microstate did not describe the behavior of all of the particles of the system. Simultaneously, different microstates were occurring in different members of the population.

In the development of the Brooks-Wiley thesis, the Shannon equation was the main measure of entropy. Of course, Boltzmann used this same equation. However, Brooks and Wiley employed the equation with a different philosophical base, and hence the equation did not serve them well.

According to traditional thermodynamic theory, the entropy of a system is influenced by its mass, and by the number of particles in the system. Since the Shannon equation expresses the diversity in the system solely in frequencies of the use of signals, there is no expression for the mass of the system, nor of the number of particles. When the Shannon equation is used in this manner, on macroscopic phenomena of diverse size, a small population with given genotypic frequencies yields the same entropy as a large population with the same genotypic frequencies, regardless of the absolute number in either population. Of course, the larger population would in fact have the greater entropy, and the margin would increase in proportion to increases in population numbers.

As an indication of the practical and theoretical implication of the omission of an expression for population size, it is noteworthy that, in chemical thermodynamics, a much used expression of entropy is calories per degree per mole. Therefore, as a measure of entropy, the Shannon equation is inappropriate when it is supplied with frequencies of microstates of the Brooks-Wiley type.

The Brooks-Wiley microstate was used to designate particular configurations in biological entities as diverse as nucleotides, genes, genotypes, individuals, populations and species (Brooks, and Wiley, 1988: 184; and Wiley, 1988: 178). All of these entities had equal status as microstates, and all made equal contributions to entropy, but each within the confines of its own model.

Fundamental to the ambiguities in the Brooks-Wiley thermodynamic model was the compromising of the microstate-macrostate distinction of the Boltzmann model. The microstates of Brooks and Wiley actually were macrostates, because each had accessible to it a very large number of Boltzmann microstates. Since the microstates were grossly open systems, subject to exchanges of energy and matter with their environments, they effectively translated themselves into series of macrostates, with the passing of time.

As mentioned above, each Brooks-Wiley microstate, being identified only by its macroscopic configuration, would be comprised of many Boltzmann microstates. This can be appreciated from the fact that typical values of  $W_{\max}$  fall between  $10^{10}$ <sup>24</sup> and  $10^{10}$ <sup>25</sup>

at 25° C. and one atmosphere for a mole of pure substances (Davies, 1972: 121). Also the number of Boltzmann microstates comprising a single Brooks-Wiley microstate would vary, even at the same level of biological hierarchy, and within a single set of comparisons. Hence, measurements on a Brooks-Wiley scale of entropy could not be converted meaningfully to the Boltzmann scale.

The measurements of Brooks and Wiley undeniably were entropy-like, but they were not close to being true measures of entropy. However, the intent of the presentation is unambiguous, and that intent proves to be sound and of major biological significance. Testing of the thesis will require a different thermodynamic model. If the Brooks-Wiley thesis is reconceptualized in terms of the Boltzmann model, a test becomes possible.

Brooks and Wiley treated information as material in form, and as existing independently of an observer (Brooks, Collier and Wiley, 1986; Brooks and Wiley, 1988: 35). In their view biological information took the form of the DNA molecules. Information was not a change in configuration of DNA, or a change in any other property which resided in DNA, such that, with the change, the DNA would decline in entropy. Information was the DNA itself.

This also was an unorthodox view, but that mattered little in the end, because Brooks and Wiley focused on the entropy of the DNA, not on its information value. Brooks, Cumming and LeBlond (1988: 201-207) measured and compared limited nucleotide sequences among species for what they called the entropy of information. The closest, but still very distant, analogue to their entropy of information is the entropy of the physical sciences, not the information of information theory. This is because the quantity in the Shannon equation increases with an increase in the number of possible signals and with an increase in the uncertainty as to which signal will appear at any moment. As such, it is analogous to a measure of the entropy of the code system. However, the critical factor missing is the entropy of the signal itself, which will differ grossly between the types of entities which Brooks and Wiley discuss.

On the other hand, information increases with a decline in the number of possible signals (states), and from a decline in the uncertainty as to which signal will appear at any one moment. In other words, the information capacity of a code is analogous on the macroscopic level to what entropy represents on the microscopic level.

In addition to failing to develop a truly thermodynamic model, Brooks and Wiley also failed to make comparisons across geologic time; nor did they scale their results in any manner having evolutionary significance. No genotypes were studied in their entirety, so all measures were partial "entropies" of information. Important unfinished business of the Brooks-Wiley exposition is to demonstrate that the entropy of information, or the chemical diversity of DNA increased during evolution. However, even such a demonstration would not be, by itself, positive proof that evolution has been towards increasing entropy.

#### FIELD TESTS OF THE BROOKS-WILEY THEORY

The lack of empirical evidence to support their thesis, of evolution towards increasing entropy, represented the most notable omission from the Brooks-Wiley presentation. However, since the initial publication of the Brooks-Wiley theory, several workers attempted to supply evidence by interpreting the results of their field studies according to certain marginal aspects of the Brooks-Wiley theory. These studies centered on the growth of the individual organism in organization and complexity (Robson, Scagel and Maze, 1988a and 1988b; Maze, Scagel and Bohm, 1987; Scagel, Maze and Bohm, 1985; and Maze, 1984), and on comparisons of intrapopulation variability with interpopulation variability (Chen, Scagel and Maze, 1986; and Robson, Scagel and Maze, 1988b).

Comparative descriptive projects potentially are valuable contributions towards an empirical test of the Brooks-Wiley theory. However, these field studies were moves in that direction only in relation to certain specialized and limited facets of the theory. Brooks and Wiley asserted not only (1) the increase in entropy with evolution, but also that (2) entropy increased with ontogenesis and (3) that mutation had primacy over selection as an evolutionary force. The design of these field studies was such that, standing alone, they served as tests only

for the second and third theses.

Given our present lack of sophistication, reliable evidence for the first thesis must span a long period of geologic time, which means that fossil evidence must be brought into the comparisons. In the context of this paper, these field studies join the body of biological evidence on evolution, from both fossils and living organisms, which has accumulated for more than one hundred years, and which must be used collectively to test the thesis of evolution towards increasing entropy.

#### EVIDENTIAL REQUIREMENTS OF THE BROOKS-WILEY THESIS

Evolutionary entropic changes can be expected to vary by species, by biotic association, by locality, and with time. It seems doubtful that anyone would claim that all evolutionary changes at all times and in all places have been either solely towards increased entropy or solely towards increased negentropy. If evolution were always towards increased entropy, how would one account for extinctions? In dwindling populations there is a decrease in biomass and a decrease in heterozygosity (i.e., in entropy of DNA through a decline in its chemical diversity)(Wright, 1977 and 1978), both of which tend to decrease the entropy of populations. These observations imply that convincing evidence for the thesis will require the demonstration of broadly-based changes.

The Brooks-Wiley theory is a macroscopic theory. It is pan-biotic in scale, both historically and geographically. It embraces all life on this planet, in all places and at all times. Consequently, studies that are local in scope, narrow in criteria, and time-shallow are by comparison microscopic, and cannot be expected by themselves to yield definitive evidence.

The point is that multiple factors affect the entropy of systems, including of populations, and an increase in the magnitude of some of these factors can be offset by a decrease in the magnitude of others. In view of our limited experience in testing the increasing-entropy thesis, all of the factors affecting entropy need be considered at the same time, with studies which are broad historically and geographically, in order to document long-term changes from evolution.

#### FACTORS WHICH INCREASE THE ENTROPY OF A SYSTEM

There are numerous types of changes in systems which will bring about an increase in the entropy of systems. These factors appear to be recognized universally by thermodynamicists, and can be abstracted from the equations of chemical thermodynamics as these equations appear in broad surveys of the field (Davies, 1972 and Waldram, 1985). According to the Boltzmann model, each of these changes results in the internal energy of systems distributing itself over time among the particles of the systems in a greater number of microstates. These changes can be identified in living systems as they can be in simple physical systems, and are applicable in a comparison of early life with existing life. Each of the following eight changes increases the entropy of systems. One manner by which the number of energy levels is increased is indicated in parentheses after each change.

1. An increase in mass. (Permits the transfer of energy in smaller increments.)
2. An increase in the internal energy. (Permits the particles to be energized in a greater variety of ways.)
3. An increase in the chemical diversity. (Permits energy to be transferred in a greater variety of increments.)

4. An increase in the mixing of chemical species. (Permits greater variety in energization and in transfer of energy.)
5. An increase in the volume. (Permits a greater variety of energizations of particles.)
6. A scattering of parts. (Diversifies the energy transfer among particles.)
7. An increase in the number of parts, such as the number of particles. (Permits a greater number of independent energizations.)
8. An easing of the constraints on a system. (Increases the latitude in the energization of particles.)

A constraint is any force which limits the magnitude of movement or the form of movement of the particles of a system. The walls of a steam chamber are constraints on the behavior of the steam's water molecules. The earth's gravity is a constraint on the movement of all systems here on earth.

All eight changes in systems which are listed above increase the number of energy levels, decrease the distance between energy levels, increase the number of energy distributions, and increase the random movement between energy distributions. Each has the effect of increasing  $W_{\max}$ , providing that all other factors either remain constant, or themselves increase in magnitude. However, these factors are not necessarily mutually exclusive, since, under given conditions, an increase in one will result in an increase in one or more of the others.

The list of entropy-altering changes in systems is in good part an outgrowth of chemical thermodynamics. It is well-suited for studies of the entropy of past and present organisms, because the features involved can be identified in living organisms, and also can be surmised from fossil evidence. This statement is not intended to minimize the technical difficulties in measuring these features. However, there is a level of uncertainty surrounding any measurement, whether or not that measurement is conducted under controlled laboratory conditions. The level of uncertainty which can be tolerated depends upon the use to which the measurement is put, and upon the nature of the conclusions to be drawn from the study.

If the differences to be observed in a study are great, there is more latitude for uncertainty in the basic measurements. For instance, in the problem at hand, the magnitude of changes over the full-course of organic evolution probably will be great enough to permit a reliance on informed estimates of the eight entropy-affecting features, and probably no direct measures of entropy will be necessary.

#### THE LONG-TERM TRENDS IN EVOLUTION

The concept that life evolved towards increasing entropy is open to more than one interpretation. However, two first meanings to everyone must be that the earliest individual organisms, on the average, were lower in entropy than organisms which are living today, and that the earliest life in its totality (as expressed through its total biomass)--over a short span of time, such as an annual cycle--was lower in entropy than is life today, over the same short span of time.

A rough numerical approximation of the relative entropy of life at the two moments in history could be tried by applying in principle Boltzmann's formula for the logarithm of  $W_{\max}$ . However, calculations of an approximate value for the number of microstates experienced by the system of life today and life living during early geologic time would be perplexing at best.



Fortunately, acceptance or rejection of the thesis of Brooks and Wiley does not require such calculations. If one applies the eight rules on increasing entropy to the long-term trends in organic evolution, the evidence is persuasive that life has increased in entropy during its evolution.

Long-term trends in organic evolution are widely known to evolutionists, since evidence of evolution has been collected for a period of more than a century. However, it is not the practice of evolutionists to compile comprehensive lists of evolutionary trends. The trends which are given below were derived in good part from the discussion of long-term "tendencies" of evolution by Simpson, Pittendrigh and Tiffany (1957: 746-749). Thus the list benefited from the collaboration of scientists who collectively were both experienced and accomplished in most of the broadly-based divisions of the biological sciences.

1. The overall biomass of life, and the average biomass of individual organisms, has increased.
  2. The cumulative internal energy of life has increased. The increase in biomass is a major factor in this increase of energy, but so too is the evolution of photosynthetic plants, and of birds and mammals.
  3. The number of individual organisms has increased, which has increased the number of parts to life and hence has increased the  $W_{\max}$  of life.
  4. The number of species has increased, which reflects an increase in the chemical diversity of life.
  5. The diversity or anatomical range of species has increased. Differentiation of parts increases the entropy of a system.
  6. The distribution of life has increased, resulting in a scattering of the system.
  7. Multicellular species have evolved, increasing the chemical diversity and chemical mixing.
  8. The cycling of minerals has increased, increasing the energization and mixing of chemical species.
  9. Life now occupies the seas, freshwater and land. Along with the evolution of benthic species, flying species, burrowing species, root systems and the trees, this reflects a scattering of life and a related increase in the volume of life.
  10. The average mobility of life probably has increased with the continued evolution of chordates and arthropods, resulting in the greater energization of life.
  11. The incidence of sympatry among species has increased, increasing the cycling of minerals and the mixing of chemicals.
  12. Focusing solely on the DNA, there has been an increase in mass, internal energy, chemical diversity, mixing of chemical species, volume, scattering of parts, and number of parts. There also has been an easing of constraints on genetic materials. Some of these conditions follow directly from the increase in mass of DNA, others from the increase in number of chromosomes.
  13. Finally, there has been a general easing of constraints on life, as reflected in its attainment of global distribution and in its occupation of a seemingly endless collection of microenvironments.
- The employment of thermodynamic concepts in the interpretation of the evolutionary tendencies from Simpson, et al. (1957) has permitted the extension of the list of trends by the addition of points which are implied by the combination of two or more items from the authors' original account. However, in my list, statements on the greater energy content of modern life originated with me (2, 10, and 12). The soundness

of these statements is dependent upon there having been no permanent drop in environmental temperature during evolution or there having been such marked increases in the total biomass of life that those increases in biomass more than compensated for any drop in temperature. All of these trends are to be taken as trends in the mean, unless the contrary is indicated.

As I interpret the fossil evidence, most of the evolutionary trends in the list could be documented by employing as few as two historical observations, if such a procedure were necessary: (a) the evolution of multicellular organisms out of single-celled forms, with the continued existence of the latter; and (b), the invasion of the land surfaces by aquatic life, with the subsequent undiminished success of aquatic life. These two observations, by themselves, demonstrate an evolutionary increase in biomass (1), diversity (5), scattering of life (6), chemical diversity (7), and volume (9). These observations also demonstrate the easing of constraints, with land habitats being added to those of the water.

If the single-celled organisms, over the long term, enjoyed undiminished success despite the advent of multicellular forms, evolutionary increases are indicated in numbers of individuals (3), numbers of species (4), cycling of minerals (8), and sympatry (11). The fact is that the evolutionary increases in the total biomass of life and in the length of food chains imply enhanced success of microorganisms.

An increase in the biomass of life indicates an increase in the cycling of minerals, as does the evolution of photosynthetic plants. The resultant increase in the flow of solar energy through life should have increased the quantity of atmospheric and crustal material circulating through life.

The evolution of multicellularity implies an increase in the chemical diversity of life and in the mixing of chemicals. With multicellularity there is a differentiation of cytoplasm between cells during growth, and errors in the replication of DNA also accumulate in the organism. One might postulate, additionally, that multicellular organisms tend to produce a greater variety of proteins than do unicellular forms.

Evidence for seven of the trends (4, 5, 6, 7, 8, 11 and 13) is provided by an increase in the number of species. In fact, an increase in the number of species lends support to all thirteen trends. Simpson and his collaborators summarized in graphic form the evidence for an evolutionary increase in the number of species.

I believe that the entropies of present-day species are fair measures of the overall degree to which they currently are distanced from the earliest of life. The advantage in using the concept of entropy for such a purpose is that it is not bound to specific structural details and hence can be applied to evolutionary changes of all types.

Equally important is the question of whether life has changed in specific entropy during its evolution. This question is much more difficult to answer, because the answer requires more refined measurements than in the case of total entropy.

There are at least two obvious measures of the departure in total entropy from the earliest life, one measure being based on the individual organism, the other being based on the entire species. In a comparison between individual organisms, founded almost exclusively on differences in biomass, some large tropical trees and the redwoods are likely to represent the most evolved living plants. Among animals the blue whale probably is the most distanced from the earliest of life. The human species is much evolved, to judge from the large individual body mass and the large numbers of organisms.

## THE RELATIONSHIP OF ENTROPY TO INFORMATION

Underlying the exposition of the Brooks-Wiley thesis was recurrent indecision on how to apply the concepts of information and entropy. Indeed, the same indecision is recurrent throughout discourse in the sciences generally, including notably the biological sciences. In my opinion, Brillouin made the fundamental contribution which will lead to a union of information theory and thermodynamics. With this assumption in mind, I will (1) describe Brillouin's key contribution, (2) extend his concept, so that I can apply it in a practical manner to a hypothetical evolutionary event, and (3) develop the philosophical considerations and the mathematical expressions which may allow the use of information theory and thermodynamic theory in a more consistent and unified manner.

Brillouin (1962) attempted to demonstrate that information was negative entropy, and in this judgement I agree with Brillouin. Brillouin's model of negative entropy began with a system in which  $W_0$  different states are possible, all with equal probability. Brillouin described this as the initial condition in which we have no special information about the general problem.

$$I_0 = 0,$$

$I_0$  being the information of the decoder. However, something occurs which gives us a more precise definition of the situation or a similar problem. Now only  $W_1$  equally probable states can occur. The information  $I_1$  was defined by Brillouin as  $K \ln (W_0/W_1)$ . Therefore,

$$I_1 = K \ln W_0 - K \ln W_1$$

where  $K$  is a constant which depends upon the units of measurement.

By adapting Brillouin's concept of information to evolutionary problems, we find that evolution not only increases the entropy of life, but also generates information. This assertion can be illustrated in the formalisms of an information theory which is classically thermodynamic. The illustration which follows has a contrived simplicity, because it is based upon a hypothetical situation. However, it is possible to apply the method to real and complex events, merely by following the same line of reasoning.

Imagine an ancestral species (A) which is destined to go through anagenesis. Suppose that there are three possible outcomes, B, B', and B". All three possible outcomes, or types of descendant species, are equally probable, and during the period in which the descendant species will be observed, each would have the capacity to go through any of  $W$  microstates. We assume that each microstate occurs only in one species, and the set of microstates in each species is unique among the species. We speak of microstate in the Boltzmann sense.

During anagenesis, the species has available  $3W$  microstates for time  $T$ . It is not known which macrostate (descendant species), and hence which set of  $W$  microstates, will prevail. This uncertainty is analogous to the uncertainty in Boltzmann's concept of entropy. According to Boltzmann, even though the entropy of a system is known and is expressed as  $K \ln W$ , with  $W$  microstates being available to the system, only one microstate actually can exist at any one time  $T$ . Of course, in the Boltzmann formulation, one particular microstate does in fact exist at a given moment, so the uncertainty resides in the ignorance of the observer as to which microstate that is.

The evolution of the descendant species, and the subsequent observation of that species, act as constraints to reduce the number of possible microstates of the evolving system to  $W$ . The information produced by the constraints is,

$$I = K \ln 3W - K \ln W.$$

Therefore,  $I = 3$ . This reasoning may be used upon systems with any number ( $N$ ) of equiprobable outcomes.

$$I = K \ln N.$$

The model postulates microstates which are preexistent to the realized configuration (macrostate). However, such a postulate is necessary in order to bring a union between thermodynamic theory and information theory, for information theory involves selection among macrostates. However, as we have seen, the postulate still maintains the classical thermodynamic perspective. It differs only in that the uncertainty of the macrostate is added to the uncertainty of the microstate. The statistical probability of the existence of any particular microstate at any given moment depends, not only on its likelihood within a given configuration, but also on the likelihood that that given configuration prevails at that given moment.

Brillouin gave his ratio a probabilistic basis by recognizing that systems of low entropy are less probable than systems of high entropy. However, this did not eliminate the need for a clear definition of the nature of Brillouin's initial condition ( $W_0$ ), against which the final condition ( $W_1$ ) is compared. Even Brillouin found it difficult to apply his equation to concrete situations. The problem arose partly from Brillouin's assumption that with  $W_0$  the existing information was zero. The value of the existing information with  $W_0$  is not zero, because  $W_0$  provides the decoder with a limit on the number of possible microstates prior to the decoding of the signal.  $K \ln W_0/W_1$  is really a measure of the change in information ( $\Delta I$ ).

However difficult it may be in practice, in theory a value for  $W_0$  always can be found for the entire code, which consists of the serially-arranged array of macroscopic events, states, items, or symbols, making up the configurations which one is studying as a system.  $W_1$  is likewise determined as the thermodynamic probability of the signal.

A principal obstacle to the synthesis of thermodynamic theory and information theory has been the symbolic nature of the signals in information theory. We tend to develop a fixation on the symbolic properties of signals, properties which seem ethereal, and we forget that every symbol has the same physical properties as are possessed by nonsymbolic physical systems.

If we remember that a signal light, a statue of bronze, ink on a page, a packet of mechanically-vibrated air molecules, carved marble, or any other signal, has ordinary physical properties, such as mass, internal energy, chemical diversity and volume, we know that any signal can be assigned a value for  $W$ --at least in theory. The sum ( $\sum W_i$ ) of all of the microstates of the signals of a code constitutes the thermodynamic probability of the code ( $W_0$ ), providing that all microstates are equally probable.

The ordinary thermodynamic procedure for determining the thermodynamic probability of several systems which are being considered collectively is to derive the product of the  $W$ 's. However, the sum is appropriate here because only one signal is decoded at any one moment, and that signal represents the state of the entire system at that moment. The microstates of different signals cannot occur simultaneously in combination.

Once the signal is decoded,  $W_0$  is reduced to the number of microstates in the signal ( $W_1$ ), as was demonstrated in the hypothetical case of anagenesis. Each time that a symbol is chosen, all other symbols, and their microstates, are excluded as possibilities for the existing state of the system.

By analogy with our example of anagenesis, before a signal is selected and decoded, any one of the  $W_0$  microstates of the code may prevail at time  $T$ . We know that  $W_0$  is equal to the collective total of all of the microstates of all of the signals of the code. This is the condition of

one's knowledge prior to decoding the signal. However, once a signal is selected and decoded at time T, only those microstates of that particular signal ( $W_1$ ) are possible. The microstates which are possible are reduced from  $W_0$  to  $W_1$ , and, if we assume that all microstates are equally probable, the change in information conveyed by the signal is

$$\Delta I = \ln W_0 - \ln W_1$$

as Brillouin predicted. This equation can be rewritten as

$$\Delta I = \ln W_0/W_1$$

Since, under these conditions,  $W_1/W_0$  is the probability of the signal, the equation is equivalent to Shannon's equation for information:

$$I = \log 1/P,$$

except that Shannon wrote his equations to the base 2, rather than to the base e.

Earlier I alluded to Shannon's formula for the entropy of a code.

$$H = -\sum P_i \log P_i .$$

where  $P_i$  represents the probability of signal i. In this equation,  $W_i/W_0$  may be substituted for the  $P_i$ 's, where the  $W_i$ 's represent the thermodynamic probabilities of the signals.

$$S = -\sum W_i/W_0 \log W_i/W_0 .$$

This equation may be rewritten.

$$S = \sum W_i/W_0 \log W_0/W_i .$$

To summarize the perspective which is being presented here, the entropy of a signal is the full entropy of the code, until the signal has been received and decoded. For instance, in the case of anagenesis, the entropy of the evolved species for time T was  $\log 3W$ , until evolution had selected a specific species (signal) of  $\log W$ . The initial uncertainty depended not only upon the number of microstates in each of the three alternative species, but also on the selection of a specific configuration.

The symbolic character to information systems already has been described as an obstacle to applying thermodynamics in the use of information theory. A second major obstacle has been the failure to carefully define the signals, their probabilities, and the limits of the code. Shannon's theory explicitly requires that the code be defined in advance, with a set of probabilities for the occurrence of signals. An example may serve to illustrate the importance of the prior assignment of probabilities to signals, and the importance of a careful definition of the code.

Brillouin described crystals at absolute zero temperature as high information systems, because they are extraordinarily improbable systems. Wicken (1983: 40-41), in a critical note on Brillouin's idea, pointed out that crystals assume only one microstate at that temperature, a microstate which therefore is absolutely certain, and which should convey no information. This apparent paradox can be dissolved by carefully defining the code in the two perspectives, and by thoughtfully assigning probabilities to the signals in the two codes.

In the first perspective (Brillouin's), the crystal is but one extremely improbable signal. It is a signal in a code which consists of an immense universe of additional signals. Under this definition of the code, the decoding of the crystal as a signal yields an enormous amount of information. With its choice as the momentary state of the system (code), the uncertainty concerning microstructure is reduced to zero. One would conjecture that the amount of information provided by the selection of the crystal would approach infinity, since the probability of the occurrence of a crystal at absolute zero temperature approaches zero.

In the second perspective (Wicken's), the crystal is not a signal, but rather is the entire code. The code is capable of but one microstate

(signal). Thus, an entire code and its single signal meet in one event. The customary physical improbability (or impossibility) of the existence of a crystal at absolute zero temperature constitutes no impediment to the theory, for the crystal is given as existing, and the only question is how much information is conveyed by its single microstate. The crystal is the predefined code, with a specified probability for its sole signal:

$$(P=1, W_0=1, \text{ and } W_1=1) \Delta I = \ln W = 0.$$

The advantage of defining  $\ln W_0/W_1$  as the change in information, rather than as total information, is apparent from these considerations.

The crystal at absolute zero temperature yields no change in information from successive decodings of its macrostructure. Therefore, it becomes the point of departure for measuring information, just as the crystal's microstructure is, in thermodynamics, the point of departure for measuring entropy. The initial observation of the macrostructure of the crystal yielded information approaching infinity. Subsequent observations of the crystal, now as a code, yield zero information, because the crystal already is known not to change in state.

Up to this point, we have in general assumed, in our expressions, that all microstates are equally probable. If all microstates are not equally probable, the complementarity which we have noted between our expressions of thermodynamic theory and information theory does not apply.

In order to correct this deficiency, it is necessary to deal with probability at two levels: first, with the probabilities of the occurrence of the macroscopic configurations which we treat as the signals that make up the code; and, second, with the probabilities of the microstates which give rise to these configurations. It is the uncertainty residing at these two levels, and also the human confusion about where the uncertainty resides, which have led to much of the indecision on how to apply thermodynamics to information problems in the sciences.

Over a century ago Boltzmann derived an equation which expressed the probability contribution of microstates to the entropy of a macroscopic configuration. It was precisely the same equation which was used later by Shannon to define the entropy of a code. Heretofore, I have referred to this equation as the Shannon equation. I now may call it the Boltzmann-Shannon equation, since the same equation which can be used to measure the average decline in entropy with the selection of a signal can also be used at the microscopic level to calculate the entropy of a system (e.g., signal). This fact provides an opportunity to write a more general equation for the thermodynamic probability ( $W_0$ ) of a code, an equation which takes into account both the numbers of microstates in the signals, and any unevenness in their probabilities.

The entropy of a system was expressed by Boltzmann as

$$H = \sum P_i \log 1/P_i,$$

where  $P_i, P_j, \dots, P_n$  are the probabilities of the microstates. This equation may be rewritten as

$$H = \sum \log (1/P_i)^{P_i},$$

which is equivalent to

$$H = \log [(1/P_i)^{P_i} (1/P_j)^{P_j} \dots (1/P_n)^{P_n}].$$

Since the entropy of a system is  $K \log W$ , the expression in brackets may be taken as the equivalent of the thermodynamic probability of the signal.

$$W_1 = [(1/P_i)^{P_i} (1/P_j)^{P_j} \dots (1/P_n)^{P_n}].$$

The entropy of the signal is  $K \log W_1$ . In this equation the product is obtained, rather than a sum, because microstates are not decoded. The probability of any one microstate at any one moment always is dependent on the overall statistical properties of the system (signal).

The code is a greater system than the signal, and is inclusive of

the signal. Its thermodynamic probability is only the sum of the W's for the signals.

$$W_0 = \sum W_i$$

The sum is taken rather than the product, because only one state of the code can occur at any one moment, and only one state can be decoded at any one moment.

The entropy of the code is

$$S = \log W_0 .$$

The information from one use of the code is

$$\Delta I = \log W_0 - \log W_1$$

Again, this result conforms to Brillouin's idea that information constitutes negative entropy.

Two properties of this approach to information are worthy of special note:

1. The definition of the code plays a strategic role in determining whether future events will produce increased entropy or increased information.
2. When all microstates are equally probable the approach often permits one to substitute probabilities for actual initial and final entropy or information measurements, as long as one is defining the magnitude of changes only. The substitution of probabilities for total entropies becomes possible because the probabilities of signals are proportional to the numbers of their microstates, providing that all microstates are equally probable within and between signals.

Even where the probabilities of microstates are not equal, changes in the entropy of systems can be measured by substituting the probabilities of signals for the entropies of signals, on the condition, however, that the probabilities of the various signals of a code can be shown to be divided proportionally to their thermodynamic probabilities.

For the biological sciences, the implications of the relationship between information and entropy are far-reaching. Historically, biologists have expended most of their effort on the creation of categories which encompass redundancy, categories such as taxa, growth cycles, adaptations, cell structures, DNA structures, and so on. These are categories which convey large amounts of information on microstructure, per unit mass. On the other hand, as yet the concept of entropy has not been applied with equal success.

If we recognize that measurements of order and disorder are mutually convertible, physical quantities of a fundamental character then become available for the study of living systems. In addition to the traditional detailed physiognomic studies of living entities, such as of cells, individuals, populations and ecosystems, systemic studies of mass, internal energy, volume, chemical diversity and constraints can be expanded. These various quantities can be related to one another systemically, and comparisons can be made with other systems. For the past several decades, procedures of this type have been developing, especially in ecology.

An advantage of the perspective which is presented here is that it renders thermodynamically open systems more amenable to study. Open systems go through changes in their internal energy and in their material bases. An orthodox physical system, which can be identified by its time-place continuity, can have its macroscopic states decoded as sources of information. Likewise, an orthodox signal system, the states of which are represented by a series of physically distinct objects (signals), can have its separate signals decoded serially as separate states of the system.

In the latter case, the material bases and internal energy of the system can be said to have changed completely with each new signal. The displacement of one physical object by another represents a change in the macroscopic state of the system, if initially the code has been so defined. The philosophical underpinnings which allow the study of such a system are no different from those which justify the study of systems which exchange energy and materials with their surroundings in small fractions. Of course, in both types of systems, the axiom still applies, that a change in information occurs only in the context of a predefined code, by whatever procedure that code may come to be defined.

In my view, there is no fundamental value in categorizing physical systems as information systems and noninformation systems, any more than it is fundamentally useful to divide systems into thermodynamic systems and nonthermodynamic systems. A particular physical system, by one definition, may be a complete code, with states which are defined as signals. By a different definition, the same system may be a signal within a more inclusive code. To the uncautious, this flexibility in the definition of signals and codes can be disconcerting.

The greater the entropy of a system, the greater the potential it offers as a code; that is, the greater is its potential for change of information with each use. This is because such a code assumes a greater number of states, each of which may be defined as a signal. On the other hand, a high entropy system offers less potential as a single signal, because its selection as the signal results in a smaller decline in the uncertainty surrounding the microstructure of the system.

In the biological sciences, a major application of information theory is to the structure of DNA. However, the employment of information theory in relation to DNA replication has been compromised because of frequent ambiguity over the signal-code distinction.

In DNA replication, complementary nucleotides often are viewed as constituting the complete code. However, complementary nucleotides constitute the entire code only in the replication of a single locus, and then only if the two noncomplementary nucleotides can, with certainty, be ruled out as possible signals. In such replications, the code consists of all possible signals, even if those signals include molecular adulterants. The amount of information conveyed in single-locus replication is extremely small, because the complementary nucleotide is virtually certain to be the signal.

Longer sequences of nucleotides take on the appearance of messages. Nevertheless, a probability for each message must be assigned, and hence each is in effect treated as a signal. All of the possible final results of replication are included as signals, whether they be just fragments, and whether they include mutations, adulterated DNA, or any other aberrations. Each possible result has a thermodynamic probability, and a probability of occurring. The sum of all of the thermodynamic probabilities of possible results represents the thermodynamic probability of the code. In order to determine the change in information which is conveyed by the replication,  $\log W_1$  (the outcome) is subtracted from  $\log W_0$  (the code).

Compared to the macroscopic systems which people are accustomed to, DNA, as a code, has a very low information capacity. In DNA replication, a single polynucleotide strand acts as an encoder, and its selections are highly predictable. The low information capacity of the DNA code also can be surmised from its small mass, small volume, limited chemical diversity and limited internal energy.

DNA is truly a "crystal" of life, around which much of the structure



of life is organized. However, on another scale, in a different code, DNA represents a considerable departure from the crystalline state of the earth's crust. That crust is the ultimate source of the materials which gave rise to life.

The thesis that life has evolved towards increasing entropy implies that the entropy of the DNA of existing life is greater than was the entropy of the DNA of the earliest life. One would expect the eight entropy-affecting quantities in DNA to have increased in evolution. One would anticipate an increase in the total number of nucleotides within living organisms, as a whole, and an increase in the average number of nucleotides within the genomes of species and within the genotypes of individuals. The mass, volume, internal energy and chemical diversity of DNA would be expected to have increased in a parallel manner.

The entropy of systems is affected strongly by increases in the number of parts. Consequently the number of DNA molecules at all levels of comparison, is an important determinant of DNA entropy. The most convenient and probably the most significant measure of increase in the entropy of heritable material is to be carried out on the properties of the chromosomal material, encompassing the properties of the DNA. The mass of chromosomal material is an essential measure, but equally important is the number of chromosomes, and their chemical diversity, including the chemical diversity of the DNA. Only the study of the intractable complete cell would be more enlightening as a source of information on the evolution of biological entropy.

In addition to the encoding of DNA, there are other levels of life activity at which encoding takes place and thereby participates in determining the nature of life in successive generations. At each level, different encoding factors (constraints) make the selection of signals. Prezygotic selection is a level in which the signals consist of the possible zygotes which could be conceived at the moment. At the population level, environmental constraints select from among all the genotypes those genotypes which will develop a reproducing phenotype. In inter-specific selection, environmental constraints, which always include the effects of other species, select the species-connected genomes that are going to increase their utilization of materials and energy at the expense of other species. All of these levels of encoding legitimately may be regarded as thermodynamic-information processes.

#### IS CLADOGENESIS THE SOURCE OF EVOLUTIONARY ENTROPY?

If evolution is towards increasing entropy, what evolutionary processes produce that entropy? Brooks and Wiley, in their rare discussions of the entropic processes of evolution, cited speciation and mutation, but included mutation as an information-producing process also (1988: 97 and Wiley and Brooks, 1982: 6). They rejected energy as an entropy-producer in evolution.

The increasing entropy of life is visible in the increasing abundance of species of undiminished number and undiminished body size, and is suggested by the vast number of branches required to graphically represent its historical development. We must ask then, is it when a species goes through cladogenesis that the additional entropy is produced?

The entropic implications of cladogenesis are of great interest in evolutionary studies because species-formation has been a key concept in evolutionary theory since its inception. Though Brooks and Wiley attributed entropy production to cladogenesis and discounted the role of energy in entropy production, in my view, Brooks and Wiley misinterpreted the entropic properties of both. Before I present my

perspective, we will see how Brooks and Wiley argued their case for cladogenetic entropy by their employment of equations and cladograms which were intended to describe hypothetical situations. Then I will address the issue by explaining why I think cladogenesis produces information, not entropy.

Undeniably it is difficult to measure directly the entropic effects of cladogenesis. Because of this difficulty in making direct measurements of entropy, Brooks and Wiley derived several equations to demonstrate an increase under hypothetical conditions (1988: 232-233). However, the increase in entropy which appeared in the equations was arbitrarily built into the entropic values which the authors assigned originally to the terms of the equation.

Each species was represented by a single term as a single microstate, without specification of the actual microstructure. No empirical evidence was presented to support the thermodynamic properties of the terms. For instance, in the equation which depicted the survival of the ancestral species through cladogenesis, Brooks and Wiley postulated an entropy for the ancestral species which was identical and unchanged from before to after speciation. This was akin to evolving the daughter species out of a system which was entirely separate from the ancestral species, and independently of the terms in the equation. One is moved to ask, What were the ecological and genetic bases for the differentiation of the new daughter species, if the ancestral species passed through the whole process in an unaltered state? The Brooks-Wiley equations left the entropic qualities of cladogenesis unresolved.

Brooks and Wiley also analyzed the entropic effects of speciation through the use of cladograms, to which increasing entropy values were assigned with each evolutionary split (1988: Fig. 4.15). Each branch of a cladogram was treated as a single independent microstate. This resulted inevitably in the descendant species collectively displaying greater entropy than the ancestral species. Actually, these cladograms can be contributory to their purpose only if they employ thermodynamic quantities to represent the conditions of cladogenesis. In this case, such a procedure was not carried out. The cladogram stated simply that one isolated genetic line became two isolated genetic lines. There was no indication of why the two descendant lines could not have been collectively of less entropy than the ancestral line.

In their philosophical development of the argument that reproductive isolation increases the entropy of populations, Brooks and Wiley relied heavily on another concept, cohesion (1988: 97; and Wiley and Brooks, 1982: 6). Cohesion and cladogenesis lie at opposite poles in a continuum.

To Brooks and Wiley, cohesion was a measure of the degree of panmixia in a population, and highly cohesive species were low in entropy because those species were "organized." In my view, Brooks and Wiley misinterpreted the entropic properties of cohesion just as they did those of cladogenesis and energy. A traditional thermodynamic interpretation of cohesion produces a picture which is quite different from theirs.

Greater cohesion results in an increase in chemical mixing, in the sense that, with panmixia, unlike genotypes are more likely to be brought together as mates. With panmixia, the microstates of heterozygotes are added to those of homozygotes. The Hardy-Weinberg Law demonstrates the greater number of heterozygotes with high cohesion. Furthermore, with panmixia the DNA is more energized, in that its carriers tend to travel more in finding their mates.

Brooks and Wiley could have found the real implications of an increase in cohesion by logically extending their conclusions on a model which they created. In this exposition, Brooks and Wiley (1988: 177)

discussed a hypothetical population which was experiencing an increase in the frequency of a mutation, X'. I believe that the logic which Brooks and Wiley applied to this hypothetical population also can be applied to the question of the entropic qualities of cohesion and speciation.

Brooks and Wiley found that the hypothetical population increased in entropy with the mutation, and they showed that the population achieved maximum possible entropy ( $\log_2 A$ ) for this single locus when all three genotypes were present, XX, XX' and X'X'. If we extend this logic by analogy to the concepts of cohesion and cladogenesis, we conclude that a species possesses greater entropy when it is cohesive than it does when it is comprised of isolated demes, for when it is cohesive, it gives expression to the maximum number of genotypes, including all possible heterozygotes.

It often is true that some time prior to, or subsequent to, reproductive isolation a species may increase in range, in numbers and in genetic diversity, all three of which contribute to the entropy of the species. However, these events are separate and distinct from simple reproductive isolation.

I believe that during species fission there is a small decline in the entropy of the species, but not in the entropy of the species and its surroundings combined. An important cause of the decline in entropy is the fact that gene flow between demes is cut off, and the opportunities for some heterozygotes are lost, not only at the locus or loci from which sterility or lack of interfertility develops, but also at all other loci where the gene frequencies of the two demes show marked contrast. Furthermore, there may be a decline in the collective fertility of two demes which are experiencing isolation. Gametes may be wasted on unproductive matings.

Perhaps it was logical for Brooks and Wiley to see cohesion as an information-increasing process, because they described speciation and reproductive isolation as entropy-producing processes. If they had assumed instead that cohesion was entropy-producing, they would have had difficulty accounting for the increasing entropy from evolution. It is my contention that the reproductive isolation of allopatric demes which have been in genetic contact decreases the entropy of the dividing system, if the reproductive isolation is unaccompanied by any other changes in the population (for the Brooks and Wiley view, see 1988: 232; Wiley and Brooks, 1982: 16; and Wiley, 1988: 184-185).

Whatever the final decision on the entropic properties of cladogenesis, it is clear that cladogenesis is not required to explain increases in the entropy of life. Life increases in entropy when one or more of the entropy-affecting factors increases, without an offsetting decline in others. Translated into the form of life processes these would include the following: offspring are conceived and grow; reproductive material mutates and the mutation is reproduced; populations grow in numbers; average individual biomass increases; metabolic rates rise; new microenvironments are occupied; individual organisms or entire species range more widely.

On the other hand, a decline in entropy occurs with the following: individuals die; selection decreases the genetic variability of a population; populations become extinct or just decline in numbers; average individual biomass declines; metabolic rates fall; old microenvironments are abandoned without replacement; and individual organisms or species range less widely. These principles of increase and decrease in entropy apply also when reference is made solely to the reproductive material.

Life would be characterized by much greater entropy today if it had been possible for it to retain all emanative mutational diversity in DNA

without ever experiencing the reproductive isolation of the species. The short-term information from cladogenesis is produced by the constraints of the environment, which permit only certain heterozygotes to reproduce. If selection had not removed from populations most of the mutations over evolutionary history, life today would not be divided into tidy species, but would consist of a collection of anomalous individuals. Without the action of selection during the very large number of generations since the origin of life, all mutants, including those with chromosomal aberrations, would have reproduced just as prolifically as did all of the actual ancestors of existing organisms, and would themselves have produced further anomalous descendants. Such an increase in diversity would have represented an increase in entropy far exceeding that which actually occurred under the constraints which produce cladogenesis.

#### ORGANIC EVOLUTION AS AN EXPRESSION OF THE SECOND LAW OF THERMODYNAMICS

Brooks and Wiley (1985: 95) concluded that it is not energy that drives evolution, but rather it is information. It would appear that this conclusion runs contrary to their major thesis, that evolution is a manifestation of the second law of thermodynamics.

By the most fundamental definition, increased entropy refers to the increased randomization of the distribution of energy in matter. Furthermore, no change in life is possible without the degradation of energy. In contrast, information is an indication of constraints on the randomization of the distribution of energy in matter. Information derives from a reduction in the number of possible states.

Consider the following thought experiment as a test of whether energy, behaving according to the second law, has been the driving force behind evolution, and behind the diversification of life. What would have happened if, several billion years ago, with the first life, essentially all sources of energy, including solar energy, had been withdrawn? Life would have taken a deeply frozen, crystalline state, close to absolute zero, and there would have been virtually no decay of the frozen system towards increasing entropy. This observation suggests that the behavior of energy, in its many forms, has been an important force in creating the present diversity of life. Has the diversification of life been due mainly to the attrition resulting from a steady flow of energy, or has it been due mainly to the effects of changes in energy flow, both locally and globally? Both possibilities are consonant with the second law of thermodynamics.

Brooks and Wiley asserted that it is structure which changes in evolution, not energy states. However, in the Boltzmann model it is impossible to have a change in structure without there being an accompanying change in energy state.

In view of the amount and variety of metabolic and ambient energy which enters, degrades in, and dissipates from living organisms, there inevitably is a continually changing energy environment for the reproductive material. Though this energy probably is mainly in the form of thermal energy, it occurs also in other forms, including chemical and mechanical. The latter is manifested in the movement of liquids, or even in the movement of chromosomes and of DNA molecules. Much of the energy in the environment of the reproductive material is likely to be random in form and magnitude, and analogous to the noise of information theory (Johnson, 1987). Since any structural change requires energy, it is difficult to escape the conjecture that mutations are powered by this energy noise.

The postulate that energy, and not information, powers the evolutionary diversification of life does not affect the other main theses in the theory of Brooks and Wiley. An important concept in the wider Brooks-Wiley theory is that, in a fundamental sense, evolution represents the unfolding of a sequence of mutational steps, the available alternatives of which are strongly modulated by the nature of DNA itself (Brooks and Wiley, 1982 and 1988). DNA can mutate only to those forms which are compatible with its structural properties as DNA, and each genotype can perform only those mutations which are compatible with its structural peculiarities.

If true, these properties of DNA necessarily limit the number of forms which life, based on DNA, can take anywhere, and also limit the sequences in which those forms can appear during evolutionary history. The number of alternate mutational pathways which in theory are available to DNA nevertheless must be very large, considering the size of DNA molecules and the number of DNA molecules found in a genotype.

Can selection be a source of diversity in evolution? It would appear that it cannot. Selection is a constraint which reduces randomness in reproduction and in phenotypic probabilities, reduces uncertainty as to both microstructure and macrostructure, and reduces entropy at all levels, from the population to the individual. Structure requires redundancy, and selection increases the redundancy in a population, both in microstructure and in macrostructure. The repetition of the same chemical, genetic, physiological, and anatomical features among individuals of a population is redundancy. Redundancy in biological features permits us to recognize taxa, such as species, genera, families and orders. The production of redundancy requires the expenditure of free energy. In the case of human populations, that free energy is spent in the trial and error process of life, culminating in some individuals being successful reproducers and others failing in reproduction.

Documented cases of the favoring of heterozygotes seem to imply that selection on occasion increases genetic diversity. However, is not this more illusion than reality? All selection is genic selection in final analysis, because of genetic reassortment in each generation due to the randomness in mating. It is possible to analyze the effects of selection at the level of the genotype, but each complete genotype remains unique in its overall constitution.

Genic selection is a result of the differences in the reproductive rates of two or more alleles. Differences between alleles in reproductive rates result from an inequality between the constraints which act on the alleles, whether those constraints be strong or weak. At equilibrium frequencies, the constraints are in balance, and there is no selection.

The equilibrium frequencies are determined by the relative fitness of the two homozygotes, and those equilibrium frequencies in turn determine the frequencies of the heterozygotes. Relative fitness of the homozygotes will determine the equilibrium frequencies whether the fitness of either homozygote or of both homozygotes is high or low. In contrast, the heterozygotes, in their reproduction, favor neither allele.

#### SUMMARY

The Brooks-Wiley thesis of evolution towards increasing entropy cannot be tested by employing the thermodynamic theory of Brooks and Wiley. The Brooks-Wiley concept of entropy leads to arbitrary and contradictory measurements, and cannot be translated into the entropy of traditional thermodynamics. A major source of ambiguity resides in their definition of microstates.

On the other hand, if the Brooks-Wiley thesis is enunciated in terms of the Boltzmann microstructure model, clearly-defined macroscopic criteria for testing the theory can be developed. When such macroscopic criteria are applied in a test of the increasing-entropy thesis, the thesis receives strong support. Consequently, it deserves the serious attention of biologists.

A comprehensive theory of evolution towards increasing entropy will require an understanding of the thermodynamic implications of cladogenesis and an understanding of the bioenergetics of mutation. In this article, the thermodynamic significance for evolution of speciation and biological energy have been discussed in a form which is consistent with the Boltzmann microstructure model. Furthermore, an effort has been made to create a philosophical and mathematical framework for common discourse on the application of information theory and thermodynamics, particularly open-systems thermodynamics, to issues of general interest in biology.

#### ACKNOWLEDGEMENTS

I would like to thank R. E. Ulanowicz, Egbert Giles Leigh, Jr., Daniel W. McShea, and Leigh Van Valen for thoughtfully commenting on the manuscript.

#### LITERATURE CITED

- Bookstein, F. L. 1983. Comment on a nonequilibrium approach in evolution. *Systematic Zoology* 32: 291-300.
- Brillouin, L. 1962. *Science and information theory*. New York. Academic Press.
- Brooks, D. R. and E. O. Wiley. 1984. Evolution as an entropic phenomenon. Pages 141-171, *in* *Evolutionary theory: Paths into the future*. (J.W. Pollard, ed.). John Wiley and Sons, Chichester.
- Brooks, D. R. and E. O. Wiley. 1985. Nonequilibrium thermodynamics and evolution: Responses to Bookstein and Wicken. *Systematic Zoology* 34: 89-97.
- Brooks, D. R. and E. O. Wiley. 1988. *Evolution as entropy: Toward a unified theory of biology*. Second edition. Univ. of Chicago Press. Chicago.
- Brooks, D. R., J. Collier and E. O. Wiley. 1986. Definitions of terms and the essence of theories: A reply to J. S. Wicken. *Systematic Zoology* 35: 641-647.
- Brooks, D. R., D. D. Cumming and P. H. Le Blond. 1988. Dollo's law and the second law of thermodynamics: Analogy or extension? Pages 189-224, *in* *Entropy, information and evolution: New perspectives on physical and biological evolution*. (B. H. Weber, D. J. Depew and J. D. Smith, eds.) MIT Press, Cambridge, Massachusetts.
- Chen, Zhong-yi, R. K. Scagel and J. Maze. 1986. A study of morphological variation in *Pseudotsuga menziesii* in southwestern British Columbia. *Canadian Journal of Botany* 64: 1654-1663.
- Davies, W. G. 1972. *Introduction to chemical thermodynamics*. W. B. Saunders Co., Philadelphia.
- Johnson, H. A. 1987. Thermal noise and biological information. *The Quarterly Review of Biology* 62: 141-152.
- Løvtrup, S. 1983. Victims of ambition: Comments on the Wiley and Brooks approach to evolution. *Systematic Zoology* 32: 90-98.
- Maze, J. 1984. A study of the factors affecting morphological differentiation in a population of *Pinus ponderosa*. *Canadian Journal of Botany* 62: 403-407.

- Maze, J., R. Scagel and L. R. Bohm. 1987. Quantitative studies in ovule development. III. An estimate of shape changes in Phyllostachys aurea. Canadian Journal of Botany 65: 1531-1538.
- Robson, K. A., R. K. Scagel and J. Maze. 1988a. Within species organization in Wyethia and Balsamorhiza and an assessment of evolutionary explanations. Taxon 37: 282-291.
- Robson, K. A., R. K. Scagel, and J. Maze. 1988b. Sources of morphological variation and organization within and among populations of Balsamorhiza sagittata. Canadian Journal of Botany 66: 11-17.
- Scagel, R. K., J. Maze, L. R. Bohm and N. L. Vogt. 1985. Quantitative studies in early ovule development. I. Intraindividual variation in Nothofagus antarctica. Canadian Journal of Botany 63: 1769-1778.
- Shannon, C. and W. Weaver. 1949. The mathematical theory of communication. University of Illinois Press, Urbana.
- Simpson, G. G., C. S. Pittendrigh, and L. H. Tiffany. 1957. Life: An introduction to biology. Harcourt Brace, New York.
- Waldram, J. R. 1985. The theory of thermodynamics. Cambridge University Press. Cambridge.
- Wicken, J. 1983. Entropy, information and nonequilibrium evolution. Systematic Zoology 32: 438-443.
- Wiley, E. O. 1988. Entropy and evolution. Pages 173-188, in Entropy, information and evolution: New perspectives on physical and biological evolution (B. H. Weber, D. J. Depew and J. D. Smith, eds.). MIT Press, Cambridge, Massachusetts.
- Wiley, E. O. and D. R. Brooks. 1982. Victims of history--A nonequilibrium approach to evolution. Systematic Zoology 31: 1-24.
- Wright, S. 1977. Evolution and the genetics of populations. Vol. 3. Experimental results and evolutionary deductions. Univ. of Chicago Press. Chicago.
- Wright, S. 1978. Evolution and the genetics of populations. Vol. 4. Variability within and among natural populations. Univ. of Chicago Press. Chicago.

