2

Growth of Order in the Universe

David Layzer

2.1 History

In 1834 a French engineer, Sadi Carnot, laid the foundation for the science of thermodynamics by proving that every ideal reversible heat engine operating between two heat reservoirs at given temperatures has the same efficiency. Carnot believed that heat is an indestructible substance. Under this assumption, he showed that if two ideal reversible heat engines operating between a given pair of heat reservoirs had different efficiencies, they could be hooked together to form a machine that would generate mechanical energy. By 1840 rigorous experiments by James Joule in England and Robert Mayer in Germany had established that, contrary to Carnot's assumption, heat is not an indestructible substance. Rather, heat and mechanical energy are interconvertible at a fixed rate of exchange. This is the First Law of thermodynamics. Around 1850 Rudolf Clausius in Germany and William Thomson in England independently revised Carnot's theory in the light of the First Law. They proved that his theorem—that all reversible heat engines operating between reservoirs at given temperatures have the same efficiency—remains valid if one introduces a new postulate. This postulate, the Second Law of thermodynamics, has two equivalent forms: (1) It is impossible to construct a device whose only effect is to convert heat from a single reservoir at uniform temperature entirely into work. (2) It is impossible to construct a device whose only effect is to transfer heat from a colder to a hotter reservoir.

In the 1850s and 1860s Clausius and Thomson developed the implications of this postulate. Thomson showed that ideal reversible heat engines can be used to define temperature in a manner that does not rely on the properties of any physical substance such as an ideal gas. Using this new definition of temperature, Clausius showed that the Second Law implies the existence of a new physical property, which he called *entropy*. This quantity remains constant in reversible changes of an isolated thermodynamic system but increases in every nonreversible change. Thus the Second Law implies that *all natural processes generate entropy*.

During the 1850s and 1860s Clausius, James Clerk Maxwell, Ludwig

Boltzmann, and others sought to relate the thermodynamic properties of macroscopic bodies, especially gases, to the dynamical behavior of their constituent molecules. At that time, molecules were still hypothetical objects, and some physicists—notably Ernst Mach—objected on methodological grounds to basing explanations of observable phenomena on a theoretical description of unobserved objects. However, the dynamical theory of gases, as it was then called, proved to have a lot of explanatory power. For a modest investment in assumptions about the properties of molecules, it yielded large returns in predictions about the macroscopic behavior of gases. Entropy, however, and with it the Second Law, remained outside the scope of the theory until Boltzmann introduced his famous statistical definition of entropy in the 1870s. Boltzmann also succeeded in deriving a special case of the Second Law from plausible statistical assumptions. Boltzmann's definition makes entropy a measure of disorder at the molecular level. The Second Law implies, therefore, that the molecular disorder of an isolated gas tends to increase until it is as large as possible. The state of maximum molecular disorder corresponds to thermodynamic equilibrium.

In 1946 Claude Shannon, following up work by Leo Szilard and others in the 1920s, explicitly freed Boltzmann's definition of entropy from its thermodynamic context and used it to construct a mathematical theory of communication. Shannon's work inspired several people to apply information theory to biological problems. These efforts were not very productive, however. Some biologists argued that the approach was wrong in principle—that neither information (as it is defined in communication theory) nor negative entropy has much to do with biological order. One of the things I hope to do in this talk is to clarify the connection between information and biological order.

2.2 What Is Entropy?

Consider a gas. Its macroscopic states are defined by variables such as temperature, density, and chemical composition, all of which represent average properties of the gas. Many different molecular configurations, or *microstates,* have the same average properties and hence represent the same macroscopic state, or *macrostate.* We may think of a macrostate as the set of all microstates that have a given set of average properties. Boltzmann defined the entropy of a macrostate as the logarithm of the number of its microstates. If H denotes the entropy of a given macrostate and W the number of microstates that belong to it—the number of ways in which the macrostate can be realized—then Boltzmann's definition reads

$$H = \log W. \tag{1}$$

If the microstates have unequal weights w_i (where the w_i are positive numbers that add up to 1), the entropy is given by

$$H = \sum w_i \log(1/w_i), \tag{2}$$

which reduces to the preceding formula when $w_i = 1/W$.

To apply Boltzmann's definition to communication theory, we identify microstates with strings of characters, and macrostates with sets of strings that share specified properties. Consider, for example, strings of English letters that have a certain length. The entropy of this set of strings is the logarithm of the number of its members. If the letters are weighted according to their frequency in some sample of English prose, we may use formula (2) to calculate the entropy. For a string of given length, this will yield a smaller value of the entropy. If we require our strings to consist of English words, we obtain a still smaller value of the entropy. And if we require the strings to be meaningful English sentences, the entropy is again smaller.

In the last example it is probably impossible to assign a precise value to the entropy, because competent judges are likely to disagree about whether certain strings of words are meaningful. But if doubtful cases constitute a small fraction of the total number of candidates the definition is still useful.

Let us now consider a biological example: the entropy of a set of variants of some biomolecule—hemoglobin, say. We may define a variant of hemoglobin as a molecule that performs the biological function of hemoglobin well enough to enable an individual that synthesizes this molecule to survive and reproduce. This definition, like the definition of a meaningful English sentence in our earlier example, is not absolutely precise. It depends on the population and the range of environments one chooses to consider. Even when these are specified it will probably be impossible to draw a line separating functional from nonfunctional molecules, just as it is impossible to draw a line separating meaningful from nonmeaningful English sentences. Here again, however, the borderline cases constitute a negligible fraction of the whole.

2.3 *What Is Information?*

The class of meaningful English sentences containing 100 or fewer characters is much smaller than the class of word-strings with 100 or fewer characters, and its members are more orderly. Reducing the entropy of a class increases the orderliness of its members. But we have to be careful. The entropy of the class of character-strings of length 5 is much smaller than the entropy of the class of English sentences of length 100 or less, but its members are less orderly. In the scientific contexts I wish to consider it is useful to define information not as negative entropy but as *the difference between* ***potential*** *entropy and* ***actual*** *entropy.*

By *potential entropy* I mean the largest possible value that the entropy can assume under specified conditions. In thermodynamics one usually specifies the values of conserved quantities such as the total energy and the number of molecules or molecular building blocks. In communication theory we may choose the specified conditions in various ways, each of which yields a different value for the potential entropy and hence a different value for the information. For example, we may choose to consider strings of English characters or strings of English words. The value we assign to meaningful English sentences of a given length will obviously depend on this choice. Analogously, in calculating the potential entropy of a gene, we may consider strings of DNA bases or strings of codons.

Potential entropy is also potential information, because the largest value that the entropy can assume under specified conditions is also the largest value that the information can assume. We can express this symmetry by writing the relation between entropy and information in the form

$$H + I = H_{\max} = I_{\max} \equiv J. \tag{3}$$

2.4 *Information and Order*

The relation between biological organization and thermodynamic order has been warmly debated for at least half a century. In the late 1930s and early 1940s Erwin Schroedinger (1944) popularized the thesis that biological organization is created and maintained at the expense of thermodynamic order, while Joseph Needham (1941) argued that "the two concepts are quite different and incommensurable. We should distinguish [Needham said] between *Order* and *Organization.*" Needham's view has been endorsed and elaborated by many biologists, including Peter Medawar (1969) and André Lwoff (1968).

The conflict between the two points of view involves several distinct issues that have not always been clearly separated.

1. *Are order and organization "different and incommensurable" at the level of physics and chemistry?* Needham and Medawar argued that they are, because when hydrogen and oxygen combine to form liquid water or when a supercooled liquid crystallizes, the thermodynamic order of the system of molecules decreases while its degree of organization increases.

This argument overlooks the fact that the thermodynamic order of a collection of molecules refers to their distribution (or, more precisely, the distribution of their representative points) in six-dimensional phase space. When a supercooled liquid crystallizes, the increase in its *spatial* order is more than offset by a decrease in the order associated with the distribution of its representative points in velocity space. Crystallization releases energy and allows the distribution to spread in velocity space. Analogously, the increase in organization that accompanies the folding of a protein or the spontaneous self-assembly of a ribosome is more than offset by the decrease in the order of the surrounding water molecules.

In short, spatial organization represents one aspect of thermodynamic order, but there are other aspects as well. The relation between spatial organization and thermodynamic order is analogous to the relation between kinetic energy and total energy.

2. *Does biological order transcend spatial organization?* For a biologist, the order of a protein is intimately bound up with its structure. A single change in the amino-acid sequence of a protein may destroy its function and hence its biological order, but from a purely chemical standpoint the protein and its nonfunctional mutant are equally orderly. Does it follow that Boltzmann's definition of order does not apply to biological order? I think not.

Consider a gas composed of oxygen-16 and oxygen-18 molecules. Is the thermodynamic order of the gas larger when the two isotopes are spatially separated than when they are mixed? The answer depends on the context. In purely chemical contexts the degree of mixing of the isotopes does not affect the entropy, because both isotopes have the same chemical properties. The order associated with the degree of mixing of the two isotopes is a separate additive component of the total thermodynamic order of the gas. Symbolically,

$$I = I_{\text{chem}} + I_{\text{mixing}}, \tag{4}$$

where the first term on the right is the part of the information that depends only on properties of the gas that do not discriminate between the two isotopes.

Analogously, we may express the information content of a functional hemoglobin molecule as the sum of a chemical contribution, which does not depend on the sequence of amino-acid residues, and a biological contribution, which does:

$$I = I_{\text{chem}} + I_{\text{bio}}. \tag{5}$$

According to our earlier discussion, the biological contribution to the information is given by the formula

$$\begin{aligned} I_{\text{bio}} &= J - H_{\text{bio}} \\ &= \log W - \log W_{\text{bio}} \\ &= \log(W/W_{\text{bio}}), \end{aligned} \tag{6}$$

where W is the number of distinct polypeptides of the same length as a functional hemoglobin molecule and W_{bio} is the number of functional variants.

We can define biological order more precisely and more generally in terms of *fitness*. Population geneticists assume that every variant of a trait can be assigned a definite (multiplicative) fitness—a measure of how effectively that trait contributes to its possessor's expectation of reproductive success under given conditions. In the preceding formula we now set W_{bio} equal to the number of variants that are at least as fit as the variant under consideration. Natural selection always increases the proportion of relatively fit variants in a population and decreases the proportion of relatively unfit variants. Hence, as I shall discuss in more detail presently, natural selection always generates biological order.

3. Some writers have argued that thermodynamic order and biological order must be fundamentally different because thermodynamic order is continually decreasing while biological order is continually increasing. Others have argued that the growth of biological order is driven by the growth of thermodynamic entropy, much as the regular oscillations of the pendulum in a grandfather clock are driven by a falling weight. Both arguments are based on a false premise: that the thermodynamic order of the universe is continually decaying. But the growth of entropy does not imply the decay of order. Remember that information, the measure of thermodynamic order, is the difference between potential and actual entropy:

$$H + I = J.$$

In thermodynamic contexts J, the potential information or entropy, is constant, but in astronomical and biological contexts it may increase with time. If J increases faster than H, information will be generated.

This point is worth emphasizing. When Eddington wrote about the "running down" of the universe, he assumed that because all natural processes generate entropy, a measure of disorder, the universe must have been more orderly in the past than it is today. Many later writers have drawn the same fallacious conclusion. The reason it is fallacious is that information, the measure of order, is not simply negative entropy. It is the difference between potential entropy or potential information (the quantity denoted above by J) and entropy (H). All natural processes generate entropy; but some processes—astronomical and biological processes in particular—also generate potential entropy. As I shall discuss presently, the universe could well have begun to expand from a state of zero entropy *and* zero information.

Let us now take a closer look at the processes that create and destroy order.

2.5 Growth of Entropy

Entropy is a measure of the spread of a discrete frequency distribution. In a gas of classical particles, the distribution is over blocks of equal size in phase space. In evolutionary contexts the distribution is over a genotype space. In a genotype space every point represents a genotype or a segment of a genotype. For example, the variants of a single gene are represented by points in a space whose dimension is equal to the number of codons.

Molecular interactions in a gas or liquid normally generate entropy. That is, they tend to distribute molecules (or rather, their representative points) as broadly as possible over phase space, if they are not so distributed to begin with. The Second Law of thermodynamics asserts that this is so. Kinetic theories, the first of which was invented by Boltzmann, seek to explain why and under what circumstances molecular interactions generate entropy.

One might suppose that any very large collection of interacting molecules would evolve toward its state of maximum entropy, but numerical simulations have shown that this is not the case. A classic example is the work of Fermi, Pasta, and Ulam, who used a computer to simulate the behavior of a long chain of coupled anharmonic oscillators. They found that the system did not relax into its state of maximum entropy but oscillated irregularly between states of high and low entropy. Thus size and complexity do not guarantee entropic behavior. On the other hand, it is easy to prove that a system of *randomly* interacting molecules evolves irreversibly toward its state of maximum entropy, provided the individual interactions are time reversible. Randomness or quasi-randomness of the underlying microscopic processes seems to be a necessary condition for entropic macroscopic behavior. The technical difficulties of kinetic theories, which need not concern us here, center on elucidating the notion of quasi-randomness in systems that are in fact completely deterministic.

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Mutation and genetic recombination play a role in biological evolution analogous to the role of molecular interactions in the evolution of a gas. The central dogma of molecular biology, that information flows unidirectionally from the genotype to the phenotype, guarantees that genetic variation is blind to its phenotypic consequences. In this sense genetic variation is random. Accordingly we may expect that *genetic variation always generates entropy*. Although I believe this to be true, it is only part of the truth. As I will discuss presently, genetic variation may also generate *potential entropy/information.*

Let me try to be more concrete. Consider the genotype space corresponding to a particular trait or group of closely related traits in a given population. Genetic variation always tends to increase the spread of genotypes in this genotype space. It does this in two ways: (a) It makes the distribution of genotypes flatter, more uniform. (b) In addition, it may allow the population to colonize previously uninhabited regions of the genotype space. The first process generates entropy but not potential entropy. Hence it necessarily destroys information. The second process generates potential entropy as well. It does not *necessarily* generate entropy. More important, it is an essential preliminary to the generation of information by differential reproduction, as I shall discuss shortly.

2.6 Growth of Potential Entropy/Information in Astronomical Contexts

In thermodynamic systems the potential entropy has a fixed value that depends on the values of appropriate conserved quantities such as the total energy. Hence the growth of entropy leads to a decline of order. In other contexts, however, the potential entropy is not fixed but may increase. If it increases faster than the entropy itself, information is generated.

Astronomy offers many examples. Let us look at a few.

1. In a star composed initially of pure hydrogen, thermonuclear reactions gradually convert hydrogen to helium in the core. The potential mixing entropy of the star thereby increases. A star of the sun's mass is stable against convection, so mixing occurs very slowly. Helium accumulates in the core, so order and information are generated.

2. In self-gravitating systems, contraction releases energy that appears partly as kinetic energy of random motions. For example, a self-gravitating gas cloud contracts and gets hotter as it radiates away energy. Thus a self-gravitating gas cloud has negative specific heat. This is a sign that it does not have a stable state of maximum entropy. (The specific heat of a system in a stable state of maximum entropy is necessarily positive.) As the gas cloud contracts, its molecules colonize new regions of velocity space. This example also illustrates how entropy growth can result in increased spatial order. As the cloud contracts, its spatial order increases, but it occupies an increasing volume of velocity space.

3. Cosmology offers the most important astronomical examples of the growth of potential entropy. In the early universe, thermodynamic equilibrium prevails locally. As the universe expands, the rates of equilibrium-maintaining reactions fall below the expansion rate and nonequilibrium conditions are frozen in. To quote from an earlier paper (1970):

> *Expansion or contraction from an initial state of thermodynamic equilibrium generates both specific entropy and specific information.* This conclusion obviously applies under much more general assumptions about the state and composition of the cosmic medium. The essential elements of the argument are (a) that the 'initial' state is one of maximum specific entropy (zero information), and (b) that the rate of cosmic

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only if classical determinism?

> expansion or contraction ... may be comparable to or greater than the rates of processes that tend to produce the state of local thermodynamic equilibrium. Because the cosmic expansion or contraction is not quasi-static, it generates departures from local thermodynamic equilibrium and hence generates information. At the same time, irreversible processes generate entropy.

Consider, for example, a uniform mixture of blackbody radiation and gas in an expanding universe. So long as the radiation and the gas exchange energy sufficiently rapidly, they remain at the same temperature, which decreases as the universe expands. Eventually, the rate of energy exchange becomes too small to keep the gas and the radiation at the same temperature. (In an initially hot universe filled with hydrogen, this happens when the hydrogen recombines, at a temperature of a few thousand degrees Kelvin. Neutral hydrogen interacts very weakly with blackbody radiation at this temperature.) Thereafter, the gas cools faster than the radiation. If there is no interaction at all between the two components, the specific entropy of each one remains constant. But because the gas and the radiation are at different temperatures, their combined entropy is smaller than it could be, given their combined energy density. In other words, the potential entropy of the cosmic medium exceeds the actual entropy, and the difference increases as the universe expands. Thus the cosmic expansion generates information.

What is going on in this example? Linear scales are increasing like a. Momentum is decreasing like $1/a$. For energy there are three possibilities: for relativistic particles $E \propto p$. For nonrelativistic particles $E \propto p^2$. For internal energy, E is constant. Hence the rate at which energy per unit mass decreases depends on the degree of equilibration between the gas and the radiation.

Consider a relativistic and a nonrelativistic gas initially in equilibrium at the same temperature. If they remain in equilibrium as the universe expands (or contracts), their common temperature varies as $(a_1/a)^q$, where a is the cosmic scale factor, a_1 is its initial value, and q is between 1 and 2. If equilibration does *not* occur, a temperature difference between the two gases develops. Thus the expansion (or contraction) generates thermodynamic order.

What happens to the entropy? If equilibration is instantaneous, the entropy per unit mass stays constant. If the two gases do not interact at all, the entropy also remains constant! If equilibration occurs subsequently, the resulting common temperature is higher than it would have been if equilibration had been instantaneous. (This is true in a contracting as well as in an expanding universe.) Thus the energy is higher than it would be if equilibration were instantaneous, and the *potential* entropy is also higher.

The rate of entropy generation is actually greatest at some intermediate (finite, nonzero) rate of equilibration.

A simple example will illustrate this conclusion. Consider two disks spinning at different rates on a common axis, as in a clutch assembly. If the disks are not in contact or if they are in contact but there is no slippage, there is no frictional dissipation. The dissipation is greatest when the disks are in contact but there is some slippage.

Because the energy per unit volume in our expanding mixture of gas and radiation is greater than it would be if equilibration were instantaneous, the cosmic expansion increases the accessible volume of phase space. If equilibration were instantaneous, the accessible volume would remain constant, the accessible region of momentum space contracting at a rate that just compensates for the expansion of physical space.

Does the growth of potential entropy distinguish between cosmic expansion and cosmic contraction? No. The preceding discussion applies equally well to a contracting universe.

Note that what *drives* the growth of chemical and structural order is the cosmic expansion (or contraction), not the tendency toward randomization. The Second Law has nothing to do with the growth of *potential* entropy. This illustrates an important general proposition:

> *Processes that generate order are in no sense driven by the growth of entropy.*

In particular, biological evolution is not driven by the growth of entropy.

4. In the preceding example, the cosmic expansion generates a temperature difference between two homogeneous components of the cosmic medium. This temperature difference could in principle be used to run a heat engine. Thus it is a potential source of free energy. By far the most important *practical* source of free energy on earth is sunlight. Sunlight is a by-product of the burning of hydrogen into helium in the deep interior of the sun. Hydrogen, in turn, was produced by chemical (more specifically, nuclear) reactions in the early universe. Let us look more closely at this process.

The rate of a two-body reaction is inversely proportional to the density and increases with increasing temperature. The cosmic expansion rate is proportional to the square root of the mass density and is independent of temperature (except insofar as thermal energy contributes to the mass density). Hence two-body reaction rates increase relative to the expansion rate as we look back in time. At sufficiently early times, the rate of any given two-body reaction will exceed the cosmic expansion rate. Conversely, the rate of any given two-body reaction eventually falls below the cosmic expansion rate.

Now consider a specific chemical equilibrium—for example, the equilibrium between neutrons, protons, electrons, positrons, neutrinos, and antineutrinos. Sufficiently early in the history of the universe, the equilibrium-maintaining reactions (e.g., the capture of an electron by a proton to give a neutron and a neutrino, and the reverse reaction) will proceed rapidly enough to keep the ratio of neutrons to protons at its equilibrium value. Eventually, however, the relevant reaction rates fall below the expansion rate. The relative abundances of the reactants are then frozen in. They retain the values appropriate to earlier values of the cosmic density and temperature.

As the cosmic density and temperature diminish, chemical equilibrium favors the formation of compound particles with progressively larger binding energies. If the expansion took place slowly enough, and if the cosmic medium remained uniform, nearly all of the matter in the universe would eventually be in the form of iron, the element with the largest binding energy per nucleon and thus the ultimate product of nuclear reactions at low temperatures and densities. In fact, chemical equilibrium is frozen in at an epoch when most of the matter is in the form of protons. That is why hydrogen is still available to produce starlight—and to support life on earth.

5. The cosmic expansion generates two important kinds of order: chemical order, which we have just discussed, and structural order. Structural order manifests itself in the *clumpiness* of the cosmic mass distribution—in the fact that matter is not uniformly distributed in space but is concentrated in a hierarchy of self-gravitating systems. Most cosmologists believe that a satisfactory cosmological theory must explain how this complicated kind of clumpiness has evolved from an initially uniform distribution of mass. Most cosmologists assume that the cosmic microwave background, a blackbody radiation field whose present temperature is 3K, is the remnant of a primeval fireball. This assumption has not so far led to a satisfactory theory for the evolution of clumpiness. The alternative cosmological assumption, that the universe began to expand from a uniform state at zero temperature, forms the starting point for a theory that predicts the gradual emergence of structure in the course of the cosmic expansion. Whether or not this theory proves to be correct, it serves to illustrate how structural order can evolve in an initially structureless universe.

2.7 Growth of Organization in Biological Evolution

Evolutionary change results from the interplay of two elementary processes: genetic variation and differential reproduction (natural selection). Molecular biology has strongly confirmed the neo-Darwinian postulate that there is no feedback of *specific* information from the living organism's life experience to variations in the genes it passes on to its descendants.

Thus genetic variation and differential reproduction are independent processes.

In the 1940s and 1950s I. I. Schmalhausen, using evidence from comparative embryology, elaborated the important thesis that evolution is a process of *hierarchic construction.* This process has two complementary aspects: *differentiation,* the increasing specialization and diversification of parts; and *integration,* the formation of new aggregates in which the structure and function of the parts are subordinated to and regulated by the structure and function of the aggregate as a whole, in the manner of cells in a tissue, tissues in an organ, or organs in an organ system. (Individual development, including psychological development, is also largely a process of hierarchic construction. This is the central idea in the work of Heinz Werner and of Jean Piaget.)

Hierarchic construction has given rise to what Stebbins, in *The Basis of Progressive Evolution,* calls a "hierarchy of complexity." Stebbins distinguishes eight major levels of overall organization in this hierarchy, represented by "free-living viroids," procaryotes, eucaryotes, sponges and fungi, flatworms and higher plants, arthropods and vertebrates, mammals and birds, and man. Each level in this hierarchy is distinguished from the preceding level by a major evolutionary innovation, and organisms on each level retain the innovations that distinguish earlier levels. Thus flatworms and higher plants are not only multicellular organisms; they also have differentiated tissues and organs. Arthropods and vertebrates have, in addition, a central nervous system and sense organs. Mammals and birds are warm-blooded, and man has the capacity for language and culture.

The "strategy" of hierarchic construction must itself be a consequence of the more elementary processes of genetic variation and differential reproduction. I have discussed the implications of this requirement elsewhere (1980). The chief implication (I have argued) is that genetic variation cannot be a completely random process, though of course it must be blind to its phenotypic consequences. For hierarchic construction to evolve as an evolutionary strategy, genetic regulation must be regulated by a genetic system that has evolved along with the genetic system that specifies an organism's development. When this idea was put forward, in 1977, several examples of genetically regulated mutation and recombination rates were known. Since then, movable genetic elements (transposons) that regulate mutation and recombination rates have been found to be ubiquitous in both procaryotes and eucaryotes.

2.8 Hierarchic Construction and the Growth of Information

To understand how evolution generates biological information, let us consider some elementary evolutionary processes.

1. *Mutation.* Consider a population whose members all carry the same variant of a gene that codes for a certain protein. Now suppose that a mutation causes a new variant of this gene to appear in some fraction of the population. The biological information associated with the new variant may be greater or less than that associated with the original one. There are two cases: (a) If the original variant is as fit as possible—if its representative point in genotype space is at a fitness peak—then any mutation decreases fitness and destroys biological information. (b) If the original variant is not as fit as possible, a mutation may increase or decrease fitness, or leave it unchanged. But the average effect of the mutation in a large population will ordinarily be to decrease fitness or to leave it nearly unchanged. Conclusion: *Mutations either diminish the average biological information associated with a given trait or leave it unchanged.*

2. *Differential reproduction* always increases the relative abundance of the fitter variants in a population and decreases the relative abundance of the less fit variants. Hence *differential reproduction always increases the average biological information associated with a given trait in a given population.*

3. *Gene duplication.* Because the duplicated genetic material is redundant, this process by *itself* alters neither the potential information nor the actual information associated with the template. But it is a necessary preliminary to the two following processes.

4. *Differentiation.* Mutations may alter copies of a duplicated segment of genetic material. Thus if A denotes a segment of genetic material, duplication may replace A by the sequence AA, and mutations may then alter this sequence to AA'. If A' were nonfunctional, this process would leave the information unchanged but would increase the potential information and the entropy (by the same factor). In reality, however, differentiation is always accompanied by

5. *Integration.* Suppose that the segment A and A' jointly take over the function of A. Among the segments AA' there may be some that are fitter than A. Natural selection now has an enlarged region of genotype space in which to act. As the frequency of the fitter variants increases, the average biological information associated with the segment AA' and its variants also increases. Gene duplication and differentiation jointly open up new regions of genotype space for colonization by an evolving population. In so doing, they create potential information. Natural selection converts this potential information into actual information.

2.9 What Drives Evolution?

It seems clear that evolution must be driven by something. Nonliving matter does not organize itself, except under very special circumstances. Even then the degree of organization attained is quite modest compared with even the simplest examples of biological organization. What is so special about living matter?

Before the advent of molecular biology, many people, including some outstanding biologists, answered this question by positing a "life force." Molecular biology and biochemistry have convincingly demonstrated that no such postulate is necessary. What distinguishes living matter from nonliving matter is "just" its organization. A virus synthesized in the laboratory would be indistinguishable from its natural template. But that does not answer the question.

A common modern answer is the growth of entropy. Evolution, on this view, is driven by the tendency of order to decay into chaos. To explain how order can result from a general tendency toward the dissolution of order, people often use the example of two unequal weights hanging on opposite sides of a pulley. As the center of mass of the two weights descends, the lighter weight rises. Analogously, protein molecules that have been denatured and then returned to their normal cellular environment spontaneously refold; the diminished entropy of the protein molecules is more than compensated by the increased entropy of the surrounding water molecules.

But we are still in the realm of analogy. To see what drives evolution we need to analyze a true evolutionary process. Consider, for example, the evolution of self-replicating strands of RNA in the well-known experiments of Sol Spiegelman. The "driving force" here is just the "Malthusian instability," the tendency of any population of self-replicators to grow exponentially so long as the supplies of building blocks and fuel molecules hold out. If two populations competing for the same building blocks and the same source of free energy have different exponential growth rates, the population with the larger growth rate will eventually take over completely. Of course, free energy and building blocks must be constantly supplied. But it would be misleading to regard the flow of free energy or of molecular building blocks as driving the evolutionary process. On the contrary, the ability of living organisms to mobilize free energy and organize matter is an evolutionary adaptation—a consequence of the reproductive instability of genetic material.

The notion that evolution is driven by the "Malthusian instability" was, of course, Darwin's key idea. If we need to be reminded of it, it is partly because generations of population geneticists have focused their studies not on instability but on statistical equilibrium. Yet, as Ernst Mayr has persuasively argued, significant evolutionary changes probably occur only, or at least primarily, in populations far from equilibrium—small, peripheral "founder" populations, where the tendency toward exponential growth is not held in check by a limited food supply, by competition, or by predation.

There is another reason why many people have been tempted to identify the driving force in evolution with the growth of entropy. We have all encountered the following argument. "Evolution, like all natural processes, rests ultimately on physical laws. All physical laws, with one exception, fail to distinguish between the two directions of time. The one exception is the Second Law of thermodynamics, which states that all physical processes generate entropy. Hence evolution, which more than any other natural phenomenon distinguishes between the direction of the past and the direction of the future, must ultimately derive its 'arrow' from the Second Law."

This argument is flawed because the Second Law is not the same kind of law as the time-reversible laws that govern elementary particles and their interactions. Those laws are independent of initial and boundary conditions. By contrast, the Second Law depends in an essential way on initial and boundary conditions. This was explicitly recognized by Maxwell, who invented a famous thought experiment to demonstrate it. Maxwell had a demon opening and shutting a trap door in a partition down the middle of a box of gas. The demon let fast molecules pass from right to left, slow molecules from left to right. Thus the temperature of the left half of the box gradually increased, while the temperature of the right half decreased, in violation of the Second Law. Half a century later, Leo Szilard pointed out that information has its price in entropy. In order to gain information about individual molecules, the demon must interact with them, and each interaction generates entropy. Szilard showed that the entropy of the system (gas molecules + demon) would increase with time, as the Second Law predicts.

It is not difficult, however, to construct a version of Maxwell's thought experiment that illustrates his original point, namely, that the Second Law presupposes certain initial (and boundary) conditions. Replace the demon by a tiny robot programmed to open and close the trap door according to the results of a calculation carried out before the start of the experiment. The calculation predicts the positions and velocities of all the molecules in the gas at any moment after the initial moment, and the robot's program allows it to use this information to do the demon's job. Of course, such a calculation would need to be based on an immense quantity of data about a still earlier state of the gas and its container, but that is all right in a thought experiment. In *this* experiment, the entropy of the system (gas molecules + robot) does decrease with time. Thus the Second Law fails if certain kinds of microscopic information about the initial state are present. This is just the sort of constraint on the Second Law that Maxwell had in mind.

Thus the Second Law presupposes the absence of certain kinds of microscopic order in the initial states of natural systems. Why these kinds of order are absent is a question that lies beyond the scope of this lecture (Layzer, 1970, 1976). The point I wish to make now is that biological

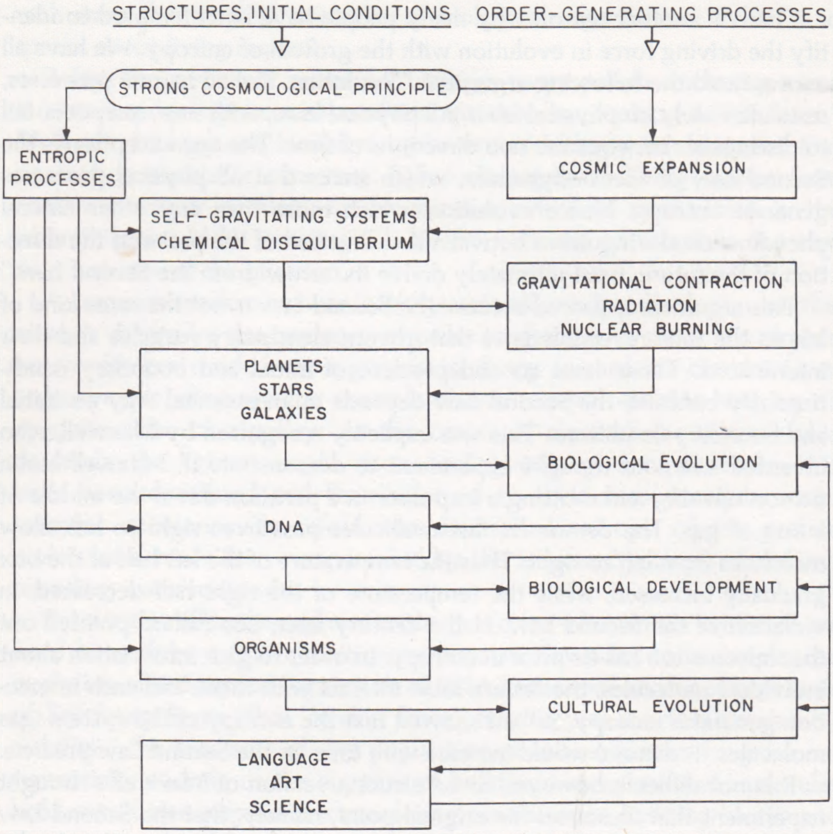

Figure 2.1
[Reproduced by permission of The MIT Press from D. Layzer, "Quantum Mechanics, Thermodynamics, and the Strong Cosmological Principle," in A. Shimony and H. Feshbach, eds., *Physics as Natural Philosophy*, Cambridge, MA: MIT Press, 1982]

evolution obviously has nothing to do with the absence of microscopic order in natural systems. Indeed, none of the order-generating processes I have discussed in this lecture depends directly on the Second Law. There is a single universal law governing processes that dissipate order, but order is generated by several hierarchically linked processes. Figure 2.1, taken from an earlier publication (Layzer, 1982), illustrates how these processes are related to each other, to the processes that generate entropy, and to a cosmic symmetry condition that I call the Strong Cosmological Principle, which supplies the initial conditions needed to derive the Second Law from the time-reversible laws of microscopic physics (Layzer, 1976).

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