NONEQUILIBRIUM THERMODYNAMICS AND EVOLUTION : A PHILOSOPHICAL PERSPECTIVE

David J. Depew

In recent years, a number of thinkers have become interested in linking biological evolution to the physics and chemistry of systems operating far from thermodynamic equilibrium. In such systems, which include entities as far apart as tornadoes and cells, order is positively rather than negatively correlated with entropy production. Non-equilibrium systems degrade the free energy in their environment, displacing their own entropy debt beyond the system itself. When the bill comes due, such systems can sometimes evolve through a phase of indeterminacy into more complex and ordered wholes, thus turning thermodynamic disaster into triumph, at least temporarily. This can occur because such systems produce internal entropy in addition to the negentropy of their interactions with the environment. Order and entropy advance together (Prigogine, 1961; Prigogine and Stengers, 1984).

The biological systems that are the direct subjects of evolutionary theory can also be seen as non-equilibrium systems. Ilya Prigogine has led the way in exploring this idea, though his concerns have been focused on the origins of genetically selfreplicating systems, and he has been reluctant to extend this investigation to the further evolution and fate of such systems. He thinks, moreover, that both pre-biotic and later phylogenetic evolution are governed by natural selection. And though natural selection can profitably be reformulated in thermodynamic terms, thermodynamics does not offer a rival causal and explanatory principle to it (Prigogine et al., 1972).

This has not, however, dissuaded others from pushing further toward a view in which non-equilibrium thermodynamics presents an alternative to natural selection. Recently, a radical proposal to link biological and physical evolution by way of nonequilibrium thermodynamics has been put forward by Daniel Brooks and E. O. Wiley (Wiley and Brooks, 1982; Brooks and Wiley, 1983, 1986). According to their theory, speciation and phylogeny are an inherent expression of the second law of thermodynamics because the systems that evolve, species, are themselves typical of systems that operate far from thermodynamic equilibrium. Moreover, phylogenetic pattern looks very like the results of just such a diachronic process as non-equilibrium thermodynamics predicts. Thus Brooks and Wiley argue that order and entropy advance together and that evolution is itself an entropic phenomenon.

Clearly an argument like this might be rhetorically effective in contending against "scientific creationists," whose primitive views about thermodynamics, based on the image of an inevitable universal heat death, lead them to think that biological order is the result of a physical miracle. But within the scientific community. Brooks' and Wiley's thesis is provoking intense and sometimes bitter disagreements. There is a question about whether what they call "informational entropy" measures anything real enough to be called entropy at all. Even if it does, the question remains how this entropic dimension is related to energetic entropy. I shall return briefly and inadequately to these questions. In this paper, however, my main concern will be to place Brooks' and Wiley's thesis within a spectrum of opinions about how non-equilibrium thermodynamics might apply to phylogenetic evolution, and to place this entire spectrum within the larger context of current debates about evolutionary theory. In this way we might learn what the consequences would be for evolutionary theory if Brooks' and Wiley's thesis turns out to be formally well-formed and materially plausible. This in turn will tell us a great deal about the current state of evolutionary theory, and help illuminate the question whether and how that current understanding is vulnerable, even if Brooks' and Wiley's particular thesis fails. This discussion, I hasten to add, will be conducted largely at a conceptual level, where philosophical analysis and criticism is most effective.

It is no secret that evolutionary theory is currently in a more agitated state than it has been since the "modern evolutionary synthesis," or Neo-Darwinism, began its triumphant rise almost fifty years ago. While Prigogine has not challenged the synthesis, or lent an ear to the many heretics in its ranks, many others have. Stephen Jay Gould and several other paleontologists have, for example, defended the view that macroevolutionary phenomena — the evolution of clades at or above the species level — cannot be accounted for in terms of the standard population-genetical models of "microevolution" that lie at the heart of Neo-Darwinism (Eldredge and Gould, 1972; Gould and Eldredge, 1977; Stanley, 1975, 1979). There is every reason to think that Brooks and Wiley intend to intervene in this and other controversies. One dimension of this effort is their attempt to establish an even more radical separation of macroevolution from microevolution than Gould and his associates have proposed, by arguing in effect that there is an autonomous non-selectionist dynamics that causally underlies macroevolution.

An examination of this claim can profitably begin by considering Brooks' and Wiley's suggestion that the anomalies now rapidly accumulating within current evolutionary theory, from fields as far apart as molecular genetics, embryology and paleontology, cannot be resolved within the basic framework or Neo-Darwinism. no matter how radically that framework is amended or, as the current phrase is, "expanded." This argument has a conceptual dimension in addition to empirical claims that can be adduced to support it. At root, Brooks and Wiley take up and develop Prigogine's own suggestion that the development of non-equilibrium thermodynamics, its application to biological objects and thus the true connection between physics and biology, has been retarded by the influence of the Newtonian paradigm on our scientific culture (Prigogine and Stengers, 1984). Brooks and Wiley argue, in effect, tht the inability of current evolutionary theory to absorb anomalies is related to the fact that the Neo-Darwinian framework too is committed, at a fundamental conceptual level, to a view of biological systems as Newtonian equilibrium systems. This is an interesting suggestion, one that deserves further explication and reflection.

The general image of a Newtonian system is that of a group of entities each of which is by nature indifferent to every other but all of which are mutually constrained into a state in which the free expression of the inherent tendencies of each is limited by its relations to all others in the system. The deepest assumption of any Newtonian system is that the forces exerted on each other by the component entities form a closed system. Because the system is closed to inputs from outside, changes in one variable necessarily imply changes in all the others. The general formulas governing these interrelated changes are called laws. The application of laws to a given system generates explanations and predictions. The general conclusion reached by inquiry into these state changes is that a Newtonian system is constantly returning to equilibrium, and will not be jarred out of that equilibrium unless a component force in the system changes, triggering a precisely predictable reordering of the system leading to a new equilibrium. It is a necessary consequence of this model that any possible state of a system is recoverable. Thus the Newtonian model does not have an inherent "arrow of time."

It would be almost impossible to exaggerate the influence of the Newtonian paradigm on our culture. We count as scientific knowledge only those interpretations of a subject matter or field the can be made to conform to it. It is true that some advanced disciplines, such as physics, have developed beyond the Newtonian paradigm. But none has advanced to mature status unless it has gone through such a phase of development. Hence there is enormous pressure to bring every area of discourse that wants to establish scientific credentials, and to wield the social power that these credentials grant, to make itself conform to this model by finding appropriate general laws and applying them to a given range of phenomena, both by giving laws-governed explanations of these phenomena and by devising practical applications. The established philosophy of science, with its stress on hypothetical deductive reasoning and the ideal of value-neutral inquiry, is but a generalized articulation of this demand. It, too, no less than the body of doctrine in each given field, shows its roots in the Newtonian paradigm, and it too connects organized inquiry to social power by granting legitimacy and authority to fields whose discursive practices have shown themselves to conform, at an important point in their development, to the Newtonian model.

The Newtonian model was initially applied to bodies whose inherent properties included mass and whose inherent tendency was to inertial motion. But since that beginning there has operated a dynamic in which the behavior of entities other than mere mass points has been treated as operating in systems strongly analogous to, and ultimately reducible to, a system of bodies. The first extension of the Newtonian paradigm was in fact to economic systems. From that time to the present economics has been dominated by equilibrium models.

In the present context, however, an even more important fact is that Darwin's theory of evolution by natural selection is itself an application of the Newtonian paradigm to the biosphere. Darwin built on Lyell's application of the paradigm to geological phenomena by attempting to demonstrate that no appeal to a non-physical agent need be invoked to explain the intricate functional unity obtaining within organisms and between organisms and their environments. By doing away with the assumption that Mayr has called "essentialism" — namely, the principle that changes in organic lineages are constrained by a set of inherent limits to such change — Darwin was able to treat each organism as an independent center of an inherent tendency toward selfpreservation; and, by way of a complex argument, to go on to conclude that organic lineages, when they do not go extinct, maintain a dynamic equilibrium with a continuously changing environment by taking up and passing on heritable variations that are eufunctional with respect to a given environment (Mayr, 1977).

Neo-Darwinism is not the same theory as Darwin's, but its claim to be a mature science rests, at the conceptual level, on its ability to more clearly project its own conformity to the Newtonian paradigm than its parent theory. Mendel's Laws, amplified to the populational level by way of the Hardy-Weinberg Equilibrium formula, state how genetic variants will be distributed in an interbreeding group when members of that group remain unaffected by a variety of exogenous forces. Without such forces, the state of the system - the proportional distribution of genetic variation in a freelv interbreeding population - will remain the same. As heritable variation occurs and is distributed in accord with Hardy-Weinberg ratios, the effect of the various forces that operate on it can be measured against a presupposed "zero-state," as forces in a Newtonian system of bodies can be measured against the zero-state of his Second Law. Elliot Sober has recently argued, in fact, that the coherence and power of the Darwinian tradition, as well as the resolution of its current problems, comes into view only when it is thus seen as a theory of Newtonian forces:

The zero force is specified by the Hardy-Weinberg Law... If no evolutionary forces act, then the frequencies of genes ... will be the same as their frequencies in the organisms of the previous generations ... Once genotypes have gone to their Hardy-Weinberg Equilibrium values, there they stay, in the absence of an evolutionary force The theory then specifies what effect each possible force will have (Sober, 1984 : 31).

Efforts have been made to treat the Hardy-Weinberg Equilibrium formula as a law of nature that can stand at the basis of a general theory of evolution. The argument for this view rests on the fact that, like all genuine laws of nature, the formula sustains counter-factuals : It tells us not what does happen, as do low-level empirical generalizations, but what would happen if certain forces did not contravene. It thus appears to have the necessity we associate with laws of nature. There are, however, a number of considerations the cast doubt on this interpretation. First, the distribution of gene frequencies in accord with the expectations of the Hardy-Weinberg formula applies only to a sub-class of biological systems, namely those that have evolved meiosis. It thus cannot stand at the basis of a fully general theory of evolution. Moreover, its necessity is compromised by its causal origins in the contingent fact of meiosis (Beatty, 1980). Secondly, it is not even universal for the class of systems to which it generally does apply. Gene copies, which abound at many chromosomal loci, can, we now know, be driven through an entire genome in ways that antecedently violate Mendel's Laws, and thus violate the Hardy-Weinberg "law", since the latter is merely a mathematical permutation of the former (Dover, 1982). This process of "molecular drive" cannot, then, be treated merely as one more of Sober's component forces. Nor can we rule out the possibility that this process has a direct role in phylogeny, in which case the latter cannot be treated merely as a long range inference from the joint operation of component forces (Campbell, 1984).

Within these limitations, however, the Hardy-Weinberg formula serves well enough for a variety of microevolutionary problems, that is, problems concerned with the fixation of variation in populations. Neo-Darwinians work in terms of a background expectation that variation is truly fortuitous with respect to the causes of fixation, and that among the causes of fixation is natural selection working in terms of environmental utility. Nonetheless, Neo-Darwinians recognize a good deal of complexity in how this picture applies to concrete cases. Variation can go to fixation without selection by way of "genetic drift." This process of random fixation becomes important to the extent that it is recognized that (1) the amount of variation that can accumulate in a population is very high; (2) populations are often not strongly panmictic, so that variants have a proportionally greater chance of going to fixation without selection as actual interbreeding is limited to and between demes; and (3) populations are not typically at or near Malthusian

limits, so that strong pressures to prune variation cannot always be presupposed. All three of these facts are now commonly acknowledged. They even play a role in the orthodox view of speciation by peripheral isolation (Mayr, 1942). This means that the problem of calculating the separate influence of the component forces can be difficult. The problem is made particularly difficult because of one of the facts we have just acknowledged. If populations were typically near Malthusian limits, as they can easily be made to be in the laboratory, then the sort of phenotypes natural selection can be expected to create can be antecedently discovered by deploying the concept of "engineering fitness" to create maximization and optimization models. The actual occurrences of these phenotypes could then be ascribed to natural selection, and other effects to presumably secondary factors. But the assumptions under which such analyses are valid cannot always be presupposed.

Recently additional considerations have been coming into view that not only make the problem of analyzing component microevolutionary forces still more complex, but suggest more directly that macroevolutionary problems cannot be regarded merely as longrun extrapolations from the operation of microevolutionary forces. I will discuss here two such considerations: (1) there are constraints on the very production of types of variation, where these constraints are themselves products of evolution; and (2) there are constraints on which level of a complex biological hierarchy composed of genes, organisms, demes and species the phenotypic effects of gene frequency changes will manifest themselves.

The idea that there are significant constraints on the very production of variation is coming out of contemporary developmental genetics (Cf. Maynard Smith et al., 1986). Developmental considerations have not been historically very important in Neo-Darwinian discourse. Some have thought that this is because a stress on gradual changes in gene frequencies under selective, and for the most part adaptational control, presupposes that the organism is a relatively decomposable system of independent traits, each of which is molded over time by the environment, whereas developmentalists have real hesitancy in regarding embryos in this atomistic way. The fact that there are historically accrued constraints on the production of variation might imply that there is long-run feedback from the environment to the germ line, even if standard anti-Lamarckian arguments are still valid for the short run. Moreover, this suggests that evolutionary directionality — the pattern carved out by evolutionary branching over a long time — may be more significantly determined by what variation is initially given than by its further determination by whatever forces act on it.

Second, we are coming to see that there are constraints not only on the source of variation but on the way its effects are channelled. Since the genome has more internal structure than had earlier been suspected, variation can sometimes be fixed at a lower level without introducing functional change at a higher. This has been demonstrated in the case of the substitution of amino acids in protein evolution (Wilson et al., 1977), but the point can easily be generalized when a robustly hierarchical view of biological systems is adopted. When changes occur in a phenotype, they may be in characteristics that are predicable of the organism in virtue of its membership in a group — a deme, a species, perhaps even a higher clade. "Group selection" lets us see that the ontology of individual competing organisms made familiar by Darwin might not be adequate for assessing the objects on which selection itself works or for whose benefit it does (Cf. Brandon and Buriau, 1984, for relevant literature).

Here we reach a point that will be important in what follows. Our brief consideration of constraints on the production and channelling of variation tends to shift the locus of explanation of evolutionary directionality from the point by point accumulation and disposition of variation to the background structure that dictates the pattern and path that process will exhibit. One crude way of putting this is that when microevolutionary forces work on an atomized collection of genes and traits and individual competing organisms "efficient causality", in the old Aristotelian sense, does the explaining. But when efficient causation works against a background of organized wholes, structural considerations (Aristotelian form, in the analogy) may give the appropriate sort of explanation.

This conceptual and methodological point leads us to see the importance of recent insistences on the internal integrity, complexity and hierarchical structure of the genome. These facts are especially evident in the regulatory gene system, which turns on and off structural gene products in accord with a developmental program. Classical Neo-Darwinism is implicitly criticized, on this view, for preserving its historically atomistic bias by relying on a tendentious picture of the relation between genes and phenotypes in which the direct connection between structural gene products (amino acids, proteins) and phenotypes, unmediated by regulatory and developmental considerations, was exaggerated. This is now changing.

From this perspective it is evident that there are constraints on the source and effects of variation just because the genome is hierarchically structured. The Darwinian hypothesis that evolution is a long-run outcome of natural selection is reasonable, then, just to the extent that these forces work, like a "tinkerer" (Jacob, 1982), on truly random variation that can be taken up into organic systems that are phenotypically decomposible into separate parts. But to the extent that constraints operate on the production of variation and on its level of fixation, we begin to understand that biological systems may not be as readily fragmented as we had thought, and that their evolutionary relationship with the environment is a complex, mediated one. If this is true, we arrive again at a conclusion already intimated : The course of evolution will not be a direct function of microevolutionary processes. Long range trends will be determined more by what variation is initially given and by what constraints serve to channel it. Thus the mere fact that every macroevolutionary effect had to have been the product of microevolutionary process does not entail that all macroevolutionary problems can be successfully answered by reference to these processes. Some questions might be answered more securely by bypassing the detailed working of microevolutionary processes and looking at the constraints that channel it.

In a sharp departure from the received philosophy of science, which identifies explanations with deductions from laws, it is now commonly acknowledged that what counts as a good explanation is directly dependent on what sort of question it responds to. The kinds of questions proper to microevolutionary studies might well regard constraints on variation and selection and other like forces as interferences in the smooth reordering of gene frequencies. But the kinds of questions proper to macroevolutionary studies might require us to treat what microevolution regards as interference as the proper causes of pattern over time. Successful explanation is a matter of measuring the real against the expected; and what is expected is largely a function of the expectations conceptually built into the theories we are using (See Garfinkel, 1981, for an incisive defense of the "relativity of explanations" and a demonstration that "structural explanations" are the only appropriate answers to some kinds of questions, questions that cannot be addressed properly by consideration of underlying "micro" causes).

A move in this direction has been made by proponents of "punctuated equilibrium" patterns in macro-evolutionary kinetics, notably S. J. Gould. Gould argues, we recall, that paleontology does not support a pattern of gradual change such as that predicted, or assumed, by the atomistic approach to traits characteristic of the Darwinian tradition. Rather, we see long patterns of stasis interrupted occasionally by periods of rapid morphological change. Gould has gone on to suggest that these facts accord better with the stress on constraints now coming from molecular genetics. He sketches an explanatory dynamics for this kinetic pattern in which sudden reorganizations in the regulatory system of the genome produce spciation prior to adaptation, followed in turn by selection among the resultant species (rather than among variant individuals within a species), the survivors of which winnowing process settle down once again into long-range morphological stasis governed by internal constraints (Gould, 1982a, b, c).

In the course of defending this view Gould has articulated the idea of an "expanded synthesis" (Gould, 1982a). He does not argue that evolution has to proceed according to his "punctuated" model; nor does he deny that some cases of speciation and subsequent phylogeny can be explained in terms of the extrapolation of combinations of micro-evolutionary forces, such as drift and organismic selection. His point is that a wide variety of models ought to be constructed, and that experience in applying such models will show over time that some are presumptively (though defeasibly) more useful for certain types of problems and processes than others. Thus further success in evolutionary biology will depend on adamant refusal to push all evolutionary problems into the procrustean bed prepared for them by the classical assumptions of the Darwinian research tradition, by the preferred models of Neo-Darwinism, and by the effort to philosophically transform the latter into a definitive and complete theory of evolution.

I will return to the methodological significance of these proposals at the end of this paper. What is important now is to see that Gould's insistence that his version of an expanded synthesis stays within the Darwinian research tradition is well taken. Though natural selection working on separate organisms will be an important part of the causal story in only a limited number of cases, natural selection itself remains conceptually at the center of Gould's proposal. Selection can operate at various levels — genes (in the sense of replicative stretches of DNA), cells, organisms, demes and species. Which level it operates on is to some extent a matter of which channels are open and which are closed by historically accrued constraints. Other processes, such as genetic drift, play auxiliary roles in matching selection to constraint. Selection occurs at those nodal points where adaptive paths are open, though this adaptation can as often occur subsequent to speciation as prior to it. Thus selection remains the central explanatory idea in Gould's expanded synthesis. In sum, its conceptual role as explanans is retained even as Gould restricts the empirical idea of gradual selection among competing individual organisms and traces the initial overextension of this model to Darwin's Victorian ideology and to the competitive capitalist society that so eagerly took up Darwin's ideas.

Despite the novelty of these ideas, therefore, Gould continues to rely on two fundamental notions in the Darwinian paradigm. First, there is genuine randomness between the level at which variation occurs and the level at which it is fixed. In the notion of "species selection," championed by Gould and Stanley, it is occurrences of speciation itself that are said to be random with respect to the direction of evolution of the clade (Cf. Stanley, 1979). This is true whether species selection is thought of in terms of differential births or differential deaths. The very idea of selection cannot dispense with this notion of randomness. Second, Gould's "expanded synthesis" remains tied to the notion of an equilibrium between the entity that is the subject of evolution and the environment. The point at which this pressure is exercised may not be the competing individual organism of Darwinian fame, and the equilibrium established may be "punctuated" rather than the instantby-instant equilibration that Darwin inherited from classical Newtonian mechanics. But, suitably mitigated and made more complex, the basic idea is still there. Perhaps for this reason such orthodox Neo-Darwinians as Avala and Stebbins have been able to argue with some plausibility that there is no need for an "expanded synthesis," since the old one accommodates most of what Gould and others have said (Stebbins and Ayala, 1981/1985).

We are finally in a position, then, to see what it would mean really to move "beyond Darwinism." It requires breaking with the two assumptions that we have just noted. What Brooks and Wiley propose does just this. Intimating that selectionism, no matter how attenuated, will distort the macroevolutionary significance of constraints, they call for a complete separation of macro- and microevolution by arguing that the long-term pattern of evolution is not

a direct function of the accumulation and selection of variation. even if that process operates through many constraints, on different objects, at different rates. It is rather a direct consequence of a law of nature dictating an inexorable accumulation of variation and a predictable pattern of its disposition over time independent of selection (Brooks and Wiley, 1983, 1986). The law in question is the second law of thermodynamics, suitably reformulated and brought to bear on genetic systems with the help of information and communication theory. The most important of these systems are species, which Brooks and Wiley take to be individuated entities held together by genetic links, as Michael Ghiselin and David Hull had already argued on conceptual grounds (Ghiselin, 1974; Hull, 1976, 1980). The evolutionary dynamics of these systems are governed by endogenous rather than imposed forces. There is an inherent "arrow of time" built into the very structures of these systems, and not caused by forces that operate on it, dictating that they will at some point enter into an "informational crisis" that breaks the bonds tying the species together along lines where constraints are weak. This occurs when permissible variation in a species, and thus informational entropy, is high while cohesion within the species deviates considerably from panmixis, for instance by marked interdemic constraints on mating. When that happens, two daughter species form up with decreased informational-entropy production in each branch but minimally greater entropy over the whole branching system. Over a protracted period of time the shape of the phylogenetic tree thus comes into view. It is the entropic nature of information transmission, together with the internal genetic constraints that keep the accumulation of variation from dissipating into chaos rather than into new forms of order, that, on Brooks and Wiley's view, is causally necessary and sufficient for this effect. As Joel Cracraft succinctly puts it, "Even in the absence of environmental complexity the accumulation of variation will lead to speciation, no doubt slowly, but nevertheless inevitably" (Cracraft, 1982 : 359). Thus Brooks and Wiley do indeed break with the two central presuppositions of the Darwinian tradition : the assumption that the occurrence of variation is random with respect to its retention, and the assumption that the retention of variation is causally due to natural selection under environmental pressure.

More concretely, this process is understood as one in which potential information accumulating in gene pools is turned into stored or expressed information by reordering of the regulatory/ developmental gene system, as Gould and others had already hypothesized. It thus comes as no surprise that some proponents of "punctuated equilibrium" have become intrigued with using Brooks' and Wiley's dynamics to explain macroevolutionary kinetics, thus switching from a selectionist paradigm that still persists, as we have seen, in the notion of an "expanded synthesis," to a new background theory rooted in non-equilibrium thermodynamics (Cf. Cracraft, 1982).

In Brooks's and Wiley's theory, there is a reversal of what is in question in evolutionary theory and what provides the explanation. Whereas Neo-Darwinians start from the assumption of stability and induce evolution, phylogenetic evolution is expected ex hypothesi on Brooks' and Wiley's model because of informational entropy. The proper question is what causes its spatial and temporal distribution. The answer is to be found in what Neo-Darwinists talk of as "constraints," which here appear as causes of macroevolutionary paths and patterns. The points made earlier, then, about the relativity of explanation should be borne in mind. These different explanatory paradigms set up what Garfinkel calls different "possibility spaces." So completely does this switch of background presuppositions justify Brooks and Wiley in thinking that they have established the autonomy of macroevolution that they might be entitled to contest Sober's claim that "When a gene in a population goes up from 54 % to 55 % on a particular Tuesday, that's also evolution" (Sober, 1984 : 31). On their view microevolution is not properly evolution at all.

This is not to say, however, that natural selection plays no role at all in Brooks' and Wiley's thesis. They argue that particular macroevolutionary contexts set up an explanatory space in which it becomes possible to ask and answer questions about how populations come to be so finely attuned to their environments. In these contexts, natural selection, as well as all other recognized microevolutionary forces, are licensed to give explanations. These explanations in turn can in principle be cited as peripherally affecting the rate and direction of speciation. In no case, however, are these processes to be cited as explaining or causing the crossing of species barriers. More generally, it becomes impossible to construct a general theory of evolution at all levels by working up from microevolutionary contexts. On the contrary, such explanations only work within boundary conditions that have been given by autonomous macroevolutionary considerations. (In this light too the notion that natural selection is best seen as a pruning force rather than as the driver of evolution might well be restored to the intuitive appeal it has always possessed.)

Finally, let us note that the same reasons that justify the claim that Brooks' and Wiley's thesis is truly non-Darwinian also justify the view that their theory is truly post-Newtonian. For the conceptual and explanatory structures at the heart of their theory do not rely on Newtonian ideas about how systems are ordered. Thus Brooks' and Wiley's most general claim is a philosophical one. They argue, in effect, that only by adopting a causal interpretation of nonequilibrium thermodynamics can we transcend the distorting effects that the Newtonian paradigm has had on evolutionary theory, a distorting effect that has reached an intolerable limit once the complexity and integrity of biological systems has been acknowledged as fully as it now has been.

Implicit in this claim, however, is another. This distortion also manifests itself in assertions commonly made by Neo-Darwinians, and especially by Mayr, that the relation between evolutionary science and physical law is a loose one. No evolutionary process, it is said, breaks physical laws; but physical laws are themselves insufficient to explain evolutionary processes (Mayr, 1984). When the laws of physics have been perceived in terms of equilibrium ideas of order, this may indeed be so. But that is at the same time a confession of the immaturity of evolutionary science, since any science that is fully mature will find progressively tighter links with the firmest accomplishments of other sciences. Brooks and Wiley claim, that is, that only by shifting toward a non-equilibrium background theory can we move evolutionary biology to the status of full maturity it has so longed to have. This status depends on being able to move from a negative view of the relation between physics and biology to a positive one. Toward an evaluation of these claims I now wish to turn.

Since its birth in the nineteenth century, thermodynamics has undergone a series of reformulations, with each reformulation moving both toward greater generality and explanatory depth. First it was seen as the study of heat dissipation in the context of the efficiency of engines. Then it was viewed as the progressive production of molecular randomness. Under the aegis of information theory, it is currently being transformed again into an even more general set of relations with a wider scope of application. Darwin encountered it in the first form. Even today creationists, the "ambulance chasers" of evolutionary science, are fond of rehearsing the headaches that Lord Kelvin gave Darwin. Darwin's buckling under to Kelvin's false prediction of a general heat death that would occur in a shorter period than Darwin required for organic evolution reveals latent physics envy in the father of modern biology. Even under the second dispensation, inaugurated by Boltzmann, evolution has been seen as violating the second law, however unjustly. But the transformation of thermodynamics into terms of information theory, as well as study of the behavior of systems operating far from thermodynamic equilibrium, have now made it easier to see why evolution is not only consistent with entropy but might itself be an entropic phenomenon.

The study of such systems owes much to the pioneering work. of Ilya Prigogine and his colleagues. Equilibrium and near equilibrium systems only do work as they move toward randomness among their microstates. In a world dominated by Newtonian ideals of science, all systems, since they are treated as equilibrium systems, are assumed to manifest this tendency. Thus systems operating far from thermodynamic equilibrium are seen as stable systems that "beat the rules" temporarily by building up order through increased degradation of their environments. What Prigogine showed was that this process can be prolonged indefinitely if enough matter and energy are pumped into the system, and that systems operating far from equilibrium produce entropy within the system itself, and not merely as a function of its interaction with its environment. As a result increasing entropy can coincide under some conditions with increasing order as such systems maintain themselves far from equilibrium.

Prigogine calls these systems "dissipative structures." Dissipative structures possess several other interesting properties. Firrst, the processes that dissipative structures undergo are time irreversible in a strong sense. The possibility of their returning, as equilibrium systems can do, to the same system state does not exist. Secondly, and in partial explanation of this fact, such systems are only "partially decomposable." They have properties that are not direct functions of the behavior of their separate parts. They are, for this reason, organized systems. Thirdly, when such systems reach a phase of instability, they move either toward dissolution or toward increased order and complexity (Prigogine and Stengers, 1984).

Convection currents and tornadoes provide Prigogine with familiar paradigms of dissipative structures. His work has been centered, however, on more intriguing and complicated cases occurring in chemical bonding, cell energetics and the origins of life. All these processes exhibit autocatalysis as a source of stable selforganization and self-perpetuation. But for Prigogine, past a certain point, when replicative fidelity is ensured, the autocatalytic selection processes that bring about living systems become more subject to classical organismic natural selection under the pressure of the environment and competition among individuals. Thus while this notion gives new grounding to natural selection as a specific form and result of autocatalysis, it does not challenge the explanatory dominance of natural selection in fully formed organic systems (Prigogine et al., 1972).

Despite Prigogine's apparent orthodoxy about phylogenetic evolution, some biologists, and notably Jeffrey Wicken, have developed his ideas about natural selection in novel ways that begin to suggest just how different natural selection might turn out to look when seen in the light of non-equilibrium thermodynamics. Wicken holds that ecological systems and their processes of autocatalytic cycling, governed by the great open energy system of the earth of which they are a part, are the fundamental context within which evolution is intelligible :

Living systems and their propagation provide particularly stable and powerful patterns of entropy production to the biosphere, and they selectively accumulate according to their ability to participate in the irreversible flow of energy from solar radiation to the sink of space (Wicken, 1984b : 495).

Because such systems are themselves dissipative structures under the influence of the energy in their boundary conditions, they inevitably produce entropy in the form not only of energy degradation but in the form of genetic variation caused by replicative error. This process can be ascribed to organisms in virtue of membership in demes or species as well as considered as separate organisms. This is the material of selection among autocatalytic units in favor of those that are environmentally efficient. A shift from equilibrium to non-equilibrium background assumptions accomplishes two important things for Wicken. It pictures evolutionary dynamics as dissipative pathways and it stresses the inevitability of the accumulation and dissipation of variation as the primary locus of evolutionary causality. That evolution occurs is a consequence of dissipation in the limited sense that without the background expectations that non-equilibrium theory grants, it is hard to see how natural selection could account for the pattern of phylogeny (Wicken, 1984b).

Darwinists, Wicken argues, with their stress on selection as a time-reversible force operating against a stable background, are continually running up against this problem, with the result that much room is given to creationists to argue that evolution itself is implausible. Like Brooks and Wiley, then, Wicken argues that this false perception is the result of an inappropriate "bottom up" strategy in evolutionary theory, and of the Newtonian atomism and reductionism that dictates this strategy. Any attempt to build up to ecological communities from genes, organisms, populations and species, each taken in independence from the energetic systems in which they are all embedded as parts, will necessarily result in placing the burden of evolutionary change on a unit that cannot bear the weight. All evolutionary theory must, then, be "top down" rather than "bottom up" (Wicken, 1982a).

From this perspective evolution is driven by the thermodynamics inherent in the physical basis of ecological communities. All such evolution is necessarily time irreversible and physically teleomatic. When a fruitless "bottom up" strategy is attempted selection will obscure the teleomatic forces that actually drive evolution. For then one must impose teleological causality on whatever level is the chosen unit to make up the explanatory debt that accrues through neglecting the whole. Teleology is, on this account, a necessary illusion accompanying any "bottom up" approach to evolution. This idea has been developed by Richard O'Grady, who argues that the equilibrium assumptions of the Darwinian tradition can generate an account of evolution only when the natural theology against which Darwin apparently revolted is conceptually smuggled into his naturalism and made covertly to do all the explanatory work (O'Grady, 1984). The outcome of such strategies, according to Wicken and O'Grady, and no doubt Brooks and Wiley too, is that Neo-Darwinists are led to protect their dubious claims to mature science by declaring the autonomy of biology from physics on the ground that the former has a teleonomic, or innocently teleological, quality absent in physical evolution (Mayr, 1984; Brandon, 1981). All this really amounts to, however, is a confession of theoretical weakness.

Recounting Wicken's views suggests just how radical Brooks'

and Wiley's own view is both in relation to classical selectionism and in relation to other accounts possible within a generally nonequilibrium framework. While the theory advanced by Brooks and Wiley relies, like Wicken's, on the notion of an inherent, timeirreversible build-up and dissipation of variation, and hence entropic disorder, in genetic systems, Brooks and Wiley treat the accumulation of variation, together with the existence of constraints on genetic decomposition, as a sufficient cause of evolution rather than as a necessary condition. Wicken makes liberal use of the part-whole relation to bring the presuppositions of both energetic and informational entropy to bear upon contexts of inquiry that continue to rely on the notion of selection, particularly for thermodynamic efficiency, as proper cause. Non-equilibrium thermodynamics grants the background presumption that makes these causal explanations go through. It does not in itself provide the explanation. Brooks and Wiley make no such use of part-whole relations, treating non-equilibrium thermodynamics in a highly abstract formulation as the cause of the accumulation and dissipation of information.

This requires them to argue on two fronts. They must oppose both the equilibrium models of Neo-Darwinism and the nonequilibrium models of their rivals. They do so by ascribing the same error to both : reliance on external causation or environmental determinism. In doing so they do not, however, display their best arguments. Prigogine's work has given rise to a conceptual distinction between "initial conditions models," which apply to systems under the control of their own history, and "boundary conditions" models, whch describe systems strongly under the influence of the synchronic forces to which they are subject at any given time. Brooks and Wiley tend to think that Neo-Darwinists as well as Prigogine and Wicken have "boundary conditions models" and that they alone have a robustly "initial conditions" model, in which the state of any species, considered as a system, is a function of its own genetic history, independent of environmental contingencies, against which species are buffered by their genomic integrity. It is not that Brooks and Wiley think that environmental, energetic conditions have no role, as necessary conditions, in allowing such systems to exist and evolve through time. Rather, they think that energy requirements for running these systems can be taken as a given and, in effect, a constant over all species, so that mentioning them as causal and explanatory considerations is improper.

NONEQUILIBRIUM THERMODYNAMICS

Nothing has drawn as much fire onto Brooks' and Wiley's head as this assertion (Wicken, 1983). Beyond its empirical questionability, however, there is a hint here of conceptual slight of hand. Prigogine's dissipative structures as well as Wicken's are initial conditions models in a real sense, since the environment does not create systems so as much as they create themselves by autocatalysis. Their behavior at any point is as much a function of their history as of their external conditions. Moreover, this view tends too much to make Neo-Darwinists into environmental determinists, whereas they too have insisted that the fate of a population is a function of its own internalized genetic history (Mayr, 1984).

Why, then, do Brooks and Wiley insist that the ineluctable accumulation of information and its dissipation through constraints is a sufficient cause of phylogeny? To understand this it is necessary to remember that Brooks and Wiley believe the link between biological systems and evolution is at the level of the species, and not at the level of any other entity in the biological hierarchy, or of any set of these entities. On the basis of this assumption, they think that the currency of evolution is the informational complexity that inevitably builds up and predictably dissipates in species. Since this process is said to occur independently of secondary mechanisms such as natural selection, which serves at best to adapt populations to local environments, Brooks and Wiley hold that phylogeny can be read off in the form of cladograms from appropriately chosen measures of informational entropy alone. This implication of their theory is in fact one of the aims that motivates it. That is one reason why they are insistent that all boundary conditions - conditions that make the successive states and fates of a system depend in a positive way on its relationship to an environment - are irrelevant, from a causal and explanatory point of view, to the inference from information accumulation and dissipation to phylogenetic order. (Another, which I will not discuss further, is their acceptance of "vicariance biogeography," which needs to minimize the effect of different energy inputs in accounting for the richness and poverty of some biota in order to argue that species distribution is a function of the earth's geological history (Cf. Cracraft, 1982). To admit any genuine causal import to external conditions as Wicken does, will block the straightforwardness of this inference. Why is preventing such a move so important to Brooks and Wiley?

Brooks' and Wiley's causal claim would, if sustained, have major consequences for the foundations of systematics. For it would

provide a basis for phylogeny in physical law, a basis that does not rest on the increasingly rickety and complex uncertainties of contemporary Darwinism. Many systematists, have in recent decades devoutly wished for precisely such an account. In particular, "phylogenetic systematists," or "cladists," have defended the view of Hennig that systematics is a science and not an art, and that the methodology of systematics requires that classification be assigned exclusively on the basis of origin, by noting successive branchings on the basis of shared and derived characters (Hennig, 1965). What is being asserted is that any systematics that depends on preestablished Linnean grades and taxa, as do Neo-Darwinist approaches to classification, retains more than a vestige of the Medieval essentialism that, as Mayr himself proclaims, modern evolutionary theory explodes. Such a systematics cannot be anything other than an art in a pejorative sense of the term.

This desire to be rigorously scientific has made ardent Popperians out of Hennig's followers. The difficulties of Neo-Darwinism have, however, driven a wedge between two branches of Hennig's school. "Transformed cladists" think that these difficulties show that it is wise for scientific systematists — against whose work evolutionary hypotheses are to be measured rather than the other way around — to stay clear of any evolutionary theory, even from commitment to the reality of evolution itself (Patterson, 1981; Cf. Beatty, 1982). Others, however, who wish to remain robustly biological, have begun a search for an evolutionary theory that, unlike Neo-Darwinism, has solid scientific credentials because it is more firmly rooted in physical principles — principles from which, in the ideal case, evolutionary theory could be deduced and on which phylogenetic systematics could be empirically grounded.

Brooks and Wiley clearly belong to the latter school. Indeed, they plainly acknowledge that their theory "is the outcome [sic] of our being systematists who adhere to a particular methodological approach called phylogenetic systematics" (Brooks and Wiley, 1986 : Preface). Brooks and Wiley have brought their general causal theory to bear on phylogenesis and classification by hypothesizing, in accord with general principles governing "dissipative structures," that entropies will be lowered in each sister species after branching, but that total entropy in the system will increase by minima. When they found apparent empirical confirmation for this hypothesis, they believed that they were justified in treating species as dissipative structures and in thinking that they had found an important positive point of contact between advanced physics and biology, in the process grounding phylogenetic systematics.

It is small wonder, then, that Brooks and Wiley have reacted strongly to environmental causality. To expose the process of phylogeny to environmental pressures in any more powerful way than the normal intraspecific fine-tuning of microevolution would be to break the chain of inferences leading directly from physics to systematics.

Brooks' and Wiley's resistance to external causes makes clear the sorts of liabilities and risks their theory has to run. We must recognize, in the first instance, that their theory is hedged about with many important conceptual claims and stipulations. Among the most important of these are the decisions to treat species as individuals and to regard them as dissipative structures; their assumption of the complete adequacy of cladistic conceptions about how to count the boundaries between one species and another; and their reliance on standard techniques of phylogenetic systematics. These and other such decisions have the effect of making Brooks' and Wiley's theory into a model. This means that the fairly straightforward inference they wish to draw from entropy production to speciation to phylogeny to systematics is pushed through much conceptual channelling and shaping. It is conceivable that robust measurements of real physical processes can emerge through such elaborate conceptual carpentering. But for that to occur these conceptual decisions must be shown to make empirical sense. The most difficult problem is whether species really are "dissipative structures" in the same sense that energetic, as distinct from informational systems, are. Can we really speak of measuring informational entropies in species?

One way to meet these difficulties would be for Brooks and Wiley to agree with some of their opponents that their informational entropies are only a rather good analogue of energetic entropies and that the way in which species are dissipative structures differs from standard examples of these. This would, in effect, be an application of abstract mathematical relations revealed by information and communication theory to genetic systems of transmission. No law of nature would be involved; or, if there were one, it would be of a biological, rather than a physical/chemical nature. One reason that might lead Brooks and Wiley to hesitate to trim their sails in this way, however, is the fact that given this move no firmer scientific foundation for systematics would be forthcoming. In fact, in response to criticisms of the initial formulation of their theory, Brooks and Wiley have moved increasingly in subsequent formulations (1983, 1986) to searching for support for their view among physicists whose own ideas about entropy support their own. They present this work as providing physical foundations for their biological conclusions. Moreover, Brooks and Wiley often intimate that one initial constraint on any new evolutionary hypothesis is that a successor theory to Neo-Darwinism should be an evolutionary biology much closer to physics. They think of their proposal as conforming to this constraint.

In order to make this idea plausible, Brooks and Wiley make three interesting suggestions. First, for evolutionary biology to be deducible from thermodynamics, thermodynamics itself will have to be reformulated at a much higher level of abstraction than at present, utilizing the resources of information theory to achieve this higher level. Second, to obviate an initially plausible objection that the four-base genetic code would long since have come to equilibrium, they stipulate that the four bases are not in fact the code, but rather are like dashes and dots in Morse code, permitting letters, words and messages to be formulated at higher combinatory levels. Third, they take an interesting view of theory reduction. The deducibility of evolutionary dynamics from reformulated thermodynamics can count as a reduction of (a part of) biology to physics only if an assumption commonly held both by proponents of biological reduction and by their autonomist enemies is rejected. Both parties usually assume that the reduction of biology to physics can be accomplished only by decomposing biological systems into least parts, between which the basic laws of physics and chemistry hold. Higher systems are aggregates of these microsystems (Cf. Rosenberg, 1985 for an up to date defense of this possibility.) In this ontological sense, Brooks and Wiley are anti-reductionist. When they say that they "hope to show more reductionist-minded workers that there are phenomena of relevance and interest in higher functional levels (populations, species)" they are rejecting the view that "adoption of a more general theory of evolution [that] has direct links to physics ... entails a reduction of biology to atomistic physical principles" (Brooks and Wiley, 1986 : Preface). But this is intended to leave open the possibility of a theoretical reduction of evolutionary biology to physics, according to which high level thermodynamic principles will generate phylogenetic evolution under specific sets of conditions, thus enabling Brooks and Wiley to claim that their theory

does make the closer link between physics and biology that any better theory requires.

This is admittedly a fascinating idea. One always likes to see unreflective assumptions questioned. But it masks uncertainties of its own. These can be seen by a quick glance at John Collier's well argued defense of Brooks and Wiley (Collier, 1985). Without waiting upon any new formulation of thermodynamics, Collier argues that information and energetic entropies are intertwined at the cellular level, and that higher level entropies are aggregates of these physically real measures. He admits that this is a "reductionist" defense of Brooks' and Wiley's claim. He must mean by this 'reductionist' in the classical fashion, based on the idea that biological systems are decomposible. In this he deviates from Brooks' and Wiley's more hierarchical view in which, in common with proponents of an expanded synthesis, biological systems are treated as forming a hierarchy or 'coordinarchy' in which higher level systems are never direct functions of lower levels, but on the contrary set up constraints and processes of "downward causation" that specify the limits in which lower level systems can operate. It is almost certainly the case that ontological reductionism is inconsistent with this hierarchical structure of the biosphere. But it may also be the case, as Collier's argument suggests, that the same reasons blocking ontological reduction also block the idea of theoretical reduction, even when the link between physical law and biology occurs well up in the hierarchy.

I present two inductive arguments for this conclusion. Wicken has taken the hierarchical vision of the biosphere from its original context within expanded New-Darwinism and reformulated it in terms of a non-equilibrium thermodynamic background. Brooks and Wiley proclaim themselves in accord with this robust sense of hierarchy, which they think is the sort of pattern that nonequilibrium processes generate over time. But closer inspection shows that what they mean is a taxonomic rather than a functional hierarchy, brought about by successive branching events. This sense of the term hierarchy is not as strongly connected with the notion of a functional hierarchy of mutually constraining levels as Brooks and Wiley think. Thus, while their argument provides grounding for their taxonomic project, it has little to do with validating the notion of a complex system of levels, though this notion is inseparable from their defense of genomic integrity.

Second, when Brooks and Wiley concede that natural selection

has a peripheral but real effect on the rate of speciation, they are saying either too little or too much. If this is consistent with the claim that entropies alone drive speciation, it says too little. But if it is taken at face value it seems to imply that the causes of rate change in speciation may enter into the total causal account that assigns weight to considerations coming from different levels. The robustly realistic sense of biological complexity that Brooks and Wiley profess, and often exhibit, will lead in the latter direction. But in this case it becomes all the more likely that there is no direct path down the deductive slope from thermodynamics to systematics.

These ambiguities are most apparent at the methodological level of Brooks' and Wiley's argument. They argue for their deduction of phylogenetics from thermodynamics by speaking of explaining phenomena by deducing them from laws plus auxiliary conditions (Brooks and Wiley, 1986 : Preface). In this view they responsor the received view of the structure of scientific theory and its account of explanation as deducibility from laws. They treat this as equivalent to the notion of causation. But, as we have seen, explanations generally and causal explanations in particular are highly context dependent affairs, and an appreciation of the complexity of biological systems is not likely to diminish out acquiescence to that context-dependence. Thus an appreciation of the complexity of the biological hierarchy is likely to be at odds with the received view of the philosophy of science. That view may help Brooks' and Wiley's phylogenetic project, but is substantively at odds with other interesting components of their work. This point could be pressed a bit further by suggesting that the notion of cause as deducibility from law is applicable only to Newtonian systems, out of consideration of which it surely grew. Newtonian systems are closed systems, and only such systems have tight enough closure conditions to make a deduction into a cause (Cf. Dyke, 1984). Nonequilibrium systems, by contrast, are radically open systems. It may well be inappropriate, then, to apply traditional philosophy of science to them. But without the introduction of such closure conditions it becomes difficult to see how Brooks' and Wiley's conclusions about systematics can follow from their basic principles.

The conclusion of the above arguments is that Brooks' and Wiley's initial and sustained concern with providing an evolutionary grounding for phylogenetic systematics inclines them toward too straightforward a deductive relationship between their thermodynamic-informational premises and their phylogenetic conclusions. But what alternatives are there to a rigorously hypothetical deductive picture if they wish to present their theory as an improvement on what, to Brooks and Wiley, looks like the theoretical regressiveness of Neo-Darwinism ?

Let us recall that when Gould defended his model of "punctuated equilibrium" by sponsoring the idea of an "expanded synthesis," he presented his view as a model that might be helpful in resolving a number of evolutionary problems, and not as a new general theory of evolution. Generalized, this means that an expanded synthesis would collect a large number of different models, which can be expected variously to apply when different conjunctions of evolutionary forces operate on different entities at various levels of the biological hierarchy under a wide variety of initial and boundary conditions. Failure of one model to account for a given case will not, then, falsify the model itself. Rather, it would call for a different model.

Gould's thought can be taken even further as a mode of exploring biological complexity. When a variety of models yield consistent and coherent information about a complex situation we arrive at what Richard Levins has called "robust theorems" (Levins, 1966). The robustness of theorems is a function of congruence among the information yielded by a variety of different approaches to the same situation or problem. Perhaps the paradigm case of robustness is the perceptual judgements that enable us to synthesize the information given by our different senses. Note too, as in this case, that robustness carries with it a presumption of the reality of the entities that we are dealing with, a presumption that famously does not accompany purely hypothetical deductive accounts, according to which events are explained when they are displayed as a consequence of a general law that covers them.

Let me call this general idea "methodological pluralism." In recnent decades, some philosophers have become interested in giving a general reformulation of philosophy of science in accord with these methodological intuitions. One expression of this is the so-called "semantic view of theories" (Giere, 1979; Suppe, 1972; Suppes, 1967). According to this view, the axiomatic heart of a solid scientific theory is not a law of nature, but rather a set of definitions in accord with which a variety of more concrete and realistic models can be constructed, which in turn are realistically interpreted when matters of particular facts accord well with them. The basic intuition is that reality and theory do not connect at the level of universal law, considered as general facts, but at the level of explanation of complex particulars.

A number of philosophers of biology whose substantive commitments are to some version or another of Neo-Darwinism have also been attracted to these notions, not only because of the difficulties attendant upon attempts to find the basic laws in biology (some of which we reviewed above in connection with the status of the Hardy-Weinberg formula), but also because of the complexity that biological systems exhibit (Beatty, 1980; Brandon, 1978). Levins' notions of "robustness" go even further under the impact of the recognition of complexity (Cf. Dyke, 1985). If these methodological ideas were to carry the day it would signal a potentially major shift in the scientific self-image of contemporary culture.

But many scientists, as well as orthodox scientistic philosophers, are more likely to see in methodological puluralism, and in the call for an "expanded synthesis," only confessions of weakness, signs that an old paradigm is coming apart because it cannot find laws to deductively cover cases. On this view methodological pluralism blurs the line between science and nonscience by using respect for complexity to disguise the possibility that a research tradition, in this case Darwinism, is in a degenerative phase. Methodological pluralism, that is, gives vice the appearance of virtue, and possibly retards the progress of science. Rather than pursuing such a line, then, evolutionary biologists should redouble their efforts to find the appropriate laws of nature from which the phenomena they seek to explain can be deduced, in conjunction with appropriate initial and boundary conditions. As a working rule, the laws that will succeed will be closer to those of physics than previous candidates, in accord with the expectations of the unity of science program and the previous success of reductionism.

It is easy to think of Brooks' and Wiley's proposal in this light. There are, however, difficulties in their theory that appear when this is done, as we have seen. It does not follow, however, that their theory should be rejected. We will do well, I believe, to acknowledge the call for a switch to non-equilibrium background principles in evolutionary science, and to move as far beyond Newtonianism as possible in the light of the current prospects for new insights. What should be rejected is the hypothetical deductivism in which Brooks and Wiley have cast their theory, a philosophy of science too closely connected with the very world-picture they wish to move beyond.

NONEQUILIBRIUM THERMODYNAMICS

This attachment to an outdated philosophy of science may well serve to protect their ideas about systematics. But it obscures the basic insight that they have so vigorously defended.

In closing, let me make one more point on behalf of preserving methodological openness when and if evolutionary theory comes to be reoriented around non-equilibrium thermodynamics. If one criterion governing the development of evolutionary theory is that a new theory should have firmer links to physics than its predecessor, another is that such a new theory should take another step toward more smoothly integrating social science with biology. Brooks, by joining in the ridicule that has been heaped upon the individualistic atomism and reductionistic determinism so evident in the sociobiology of E.O. Wilson and others, has acknowledged this criterion (Brooks, 1983). But it does not seem clear that his and Wiley's exclusive stress on the fate of species as a whole tells us much about how to bring the thermodynamic perspective to bear on social questions. By contrast, Wicken has proclaimed that his own more pluralistic approach suggests "a connection between biology and human values ... different ... than ... sociobiology. Normative frameworks are cultivated within the context of individual-as-thermodynamic system in nutritive interaction with a hierarchy of higher order thermodynamic systems : family, community, ecosphere, biosphere" (Wicken, 1984: 499).

C. Dyke has explored this perspective by treating cities as thermodynamically open systems (Dyke, unpublished). In this view, higher order ideological systems do not have to be treated as blind reflexes of reducing economic forces. On the contrary, the rich panoply of human practices, institutions and beliefs are not only conditions for the preservation and expansion of economic systems but are themselves partly constitutive of the distinctively human economic systems that we call cultures and civilizations. Non equilibrium thermodynamics, interpreted in terms of methodological pluralism, may finally lead us to the sort of non-reductionistic naturalism that allows us to see this.

California State University, Fullerton

ACKNOWLEDGEMENTS

This paper owes a great deal to C. Dyke and B. Weber. I am also grateful to R. Burian. A much earlier version was given at the Second Summer Conference on History, Philosophy and Sociology of Biology, St. Mary's College, Indiana, June 1985. Robert Brandon cured me of one error on that occasion. But error, as Aristotle says, is infinite. For the many errors in this paper only I am to blame. Dan Brooks and Jeff Wicken have been very generous in discussing their work, especially on the occasion of a conference on non-equilibrium evolution held at California State University, Fullerton in April of 1985, sponsored by the University's School of Mathematics, Science and Engineering.

REFERENCES

··-, 2

BEATTY, J., (1982), "Classes and cladists."

- BEATTY, J., (1980), "What's wrong with the received view of evolutionary theory". PSA 2, 397-426.
- BOOKSTEIN, F., (1983), "Comment on a 'nonequilibrium' approach to evolution". Syst. Zool. 32, 291-300.
- BRANDON, R., (1978), "Adaptation and evolutionary theory". Stud. Hist. Phil. Sci. 9, 181-206.
- BRANDON, R., (1981) . "Biological teleology: questions and answers." Stud. Hist. Phil. Sci. 12, 91-105.
- BRANDON, R. and R. BURIAN, (1984), Genes, Organisms and Populations: Controversies Over the Units of Selection. MIT Press/Bradford Books, Cambridge, Mass.
- BROOKS, D.R., (1983), "What's going on in evolution?" Can J. Zool. 61, 2637-2645.
- BROOKS, D.R. and E.O. WILEY, (1983). "Evolution as an entropic phenomenon." In: *Evolutionary Theory: Paths to the Future.* edited by J.W. Pollard, John Wiley and Sons, London.
- BROOKS, D.R. and E.O. WILEY, (1985), "Nonequilibrium thermodyanmics and evolution: responses to Bookstein and Wicken." Syst. Zool. 34, 89-97.
- BROOKS, D.R. and E.O. WILEY, (1986), Evolution as Entropy: Toward a Unified Theory of Biology. University of Chicago Press, Chicago.
- CAMPBELL, J., (1984), "An organizational interpretation of

evolution" in *Evolution at a Crossroads.* edited by Depew, D. and B. Weber. MIT Press/Bradford Books, 1984.

- COLLIER, John, (1985) ."Entropy and evolution". Philosophy of Biology 1.
- CRACRAFT, J., (1982), "A nonequilibrium theory for the rate control of speciation and extinction and the origin of macroevolutionary patterns". Syst. Zool. 31 (4), 348-365.
- DOVER, G., (1982), "Molecular drive : a cohesive mode of species evolution". *Nature 299*, 111-117.
- DYKE, C., (1984), "Complexity and closure." In: *Evolution at a Crossorads.* edited by Depew, D. and B. Weber, MIT Press/ Bradford Books, Cambridge, Mass.
- ELDREDGE, N. and S.J. GOULD, (1972), 'Punctuated equilibrium: an alternative to phyletic gradualism.'' In: *Models of Paleobiology*. edited by Schopf, T.J.M. W.H. Freeman, San Francisco.
- GARFINKEL, A., (1981), Forms of Explanation. Yale University Press, New Haven, Conn.
- GHISELIN, M.T., (1974), "A radical solution to the species problem." Syst. Zool. 23, 536-544.
- GIERE, R., (1979), Understanding Scientific Reasoning. New York: Holt, Rinehart, and Winston.
- GOULD, S.J., (1982a), 'Darwinism and the expansion of evolutionary theory." Science 216, 380-386.
- GOULD, S.J., (1982b), 'The meaning of punctuated equilibrium and its role in validating a hierarchical approach to macroevolution." In *Perspectives in Evolution*, edited by Milkman, R. Sinauer, Sunderland, Mass.
- GOULD, S.J., (1982c), "Change in developmental tuning as a mechanism of macroevolution." In: *Evolution and Development*, edited by Bonner, J. T. Springer Verlag, Heidelberg.
- GOULD, S.J. and N. Eldredge, (1977), "Punctuated equilibrium: the tempo and mode of evolution reconsidered". Paleobio. 3, 115-151.
- GOULD, S.J. and R.C. LEWONTIN, (1978), "The spandrels of San Marco and the Panglossian paradigm : a critique of the adaptationist program." Proc. Roy. Soc. Lon. B 205 : 581-598. Reprinted in Conceptual Issues in Evolutionary Biology, 1984, edited by Sober, E. MIT Press/Bradford Books, Cambridge, Mass.

HENNIG, W., (1965), "Phylogenetic systematics", Ann. Rev. Ent.

10, 97-116. Reprinted in *Conceptual Issues in Evolutionary Biology*. 1984. Edited by Sober, E. MIT Press/Bradford Books, Cambridge, Mass.

HULL, D., (1976), "Are species really individuals?" Syst. Zool. 25, 174-191.

HULL, D., (1980), "Individuality and selection". Ann Rev. Ecol. System. 11, 311-312.

JACOB, F., (1982), The Possible and the Actual. University of Washington Press, Seattle.

LOVTRUP, S., (1983), "Victims of ambition: comments on the Wiley and Brooks approach to evolution." Syst. Zool. 32, 90-92.

LANDSBERG, P.T., (1984) ."Can entropy and 'order' increase together ?" *Physics Letters. 102A*, 171-173.

LEVINS, R., (1966) ."The strategy of model building in population biology." Am. Sci. 54, 421-431.

MAYNARD SMITH J., R. BURIAN, S. KAUFFMAN, P. ALBERCH, J. CAMPBELL, B. GOODWIN, R. LANDE, D. RAUP, L. WOLPERT, (1985), "Developmental constraints and evolution". Quart. Rev. Biol.

MAYR, E., (1942), Systematics and the Origin of Species, Columbia University Press, New York.

MAYR, E., (1977), "Darwin and natural selection." Am. Sci. 65, 321-7.

MAYR, E., (1984), "How biology differs from the physical sciences" In Evolution at a Crossroads. Edited by Depew, D. and B. Weber, MIT Press/Bradford Books, Cambridge, Mass.

O'GRADY, R., (1984), "Evolutionary theory and teleology". J. Theor. Biol. 107, 563-578.

PATTERSON, C., (1981), "Cladistics". Biologist 27, 234-240.
PRIGOGINE, I., (1961), Introduction to Thermodynamics of Irreversible Processes, 2nd ed., John Wiley, New York.

PRIGOGINE I., G. NICOLIS and A. BABLOYANTZ, (1972), "Thermodynamics of evolution". *Physics Today* 25 (11), 23-278; 25 (12), 38-44.

PRIGOGINE, I. and I. STENGERS, (1984), Order Out of Chaos. Bantam Books, Toronto and New York.

ROSENBERG, A., (1984), The Structure of Biology. Cambridge University Press, Cambridge.

SOBER, E., (1984), The Nature of Selection. MIT Press/Bradford Books, Cambridge, Mass.

STANLEY, S., (1975), "A theory of evolution above the species level". Proc. Nat. Acad. Sci. 72, 647-650.

- STANLEY, S., (1979), Macroevolution: Pattern and Process. W.H. Freeman, San Francisco.
- STEBBINS, L. and F. AYALA, (1981), "Is a new evolutionary synthesis necessary ?" Science 213, 967-971.
- STEBBINS, L. and F. AYALA, (1985), "The evolution of Darwinism", Sci Am.
- SUPPE, F., (1972), "The search for philosophic understanding of scientific theories." In: *The Structure of Scientific Theories*, edited by F. Suppe. Urbana: University of Illinois Press.
- SUPPES, P., (1967), "What is a scientific theory ?" In: *Philosophy* of Science Today, edited by S. Morgenbesser. New York: Basic Books.

WICKEN, J.S., (1979) "The generation of complexity in evolution: a thermodynamic and information-theoretical discussion, J. Theor. Bio. 77, 349-365.

- WICKEN, J. S., (1980), "A thermodynamic theory of evolution". J. Theor. Bio. 87, 9-23.
- WICKEN, J.S., (1983), "Entropy, information and nonequilibrium evolution". Syst. Zool. 32, 438-443.
- WICKEN, J.S., (1984a), "Autocatalytic cycling and self-organization in the ecology of evolution". Nature and System 6, 119-135.
- WICKEN, J.S., (1984b), "The cosmic breath : reflections on the thermodynamics of creation". Zygon 19, 487-505.
- WILEY, E.O., and D.R. BROOKS, (1982), "Victims of history: a nonequilibrium approach to evolution". Syst. Zool. 31, 1-24.
- WILEY, E.O. and D.R. BROOKS, (1983), "Nonequilibrium thermodynamics and evolution : a response to Lovtrup". Syst. Zool. 32, 209-219.
- WILSON, A.C., S. CARLESON, and T. J. WHITE, (1977), "Biochemical evolution". Am. Rev. Biochem. 46, 573-639.