

CHALLENGES TO THE EVOLUTIONARY SYNTHESIS

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Neo-Darwinism has been rightly construed more as a treaty than a theory because it laid down terms that allowed evolutionists and practitioners of the new science of genetics (and more generally molecular biology) to work together under common presuppositions. Evolutionists, in repudiation of their earlier flirtations with Lamarckism, accepted Weismannism; while geneticists, abandoning stress on macromutations, accepted the gradualist assumptions of the Darwinian tradition (Mayr and Provine, 1980). What made these agreements possible was a common analytical framework based on the amplification of Mendel's Rules to the level of populations by way of the Hardy-Weinberg Equilibrium Formula, according to which gene frequencies could be presumed to remain the same over successive generations unless and until exogenous forces caused one genetic variant to be preferred to another.

Depew and Weber, (1988, p. 317)

The term 'evolutionary synthesis' was introduced by Julian Huxley in *Evolution: the Modern Synthesis* (1942) to designate the general acceptance of two conclusions: gradual evolution can be explained in terms of small genetic changes ('mutations') and recombination, and the ordering of the variation by natural selection; and the observed evolutionary phenomena, particularly macroevolutionary processes and speciation, can be explained in a manner that is consistent with the known genetic mechanisms.

Mayr in Mayr and Provine, 1980, p. 1, quoted in Eldredge, p. 5

Our goal [in soliciting these essays] is to examine what contributions, if any, can be made by a philosophical reexamination of the underlying assumptions implicit in classical and current evolutionary theory. Is evolution at a crossroads, paraphrasing the title of a recent book? If it is, what alternative assumptions will best guide future research on evolution into new and fruitful directions?

Max Hecht, from the letter inviting this essay

Introduction

This essay offers a perspective on some current disputes regarding the nature and value of the evolutionary synthesis and the theoretical foundations of evolutionary theory.¹ I agree with Depew and Weber's characterization: the synthetic theory of evolution is *not* mainly a predictive or retrodictive theory, but a *treaty* favoring work within the confines of a particular research

¹ The present article is an essay review of four books, namely Eldredge (1985), Ho and Saunders (1984), Pollard (1984), and Reid (1985). These volumes will be cited without date references; all other citations will include dates. I have taken Max Hecht's inquiry, used as an epigraph, seriously; accordingly I have looked far beyond these books in discussing the content, value, and status of the so-called synthetic theory of evolution.

program. In other words, the synthetic theory is better viewed as a supra-theoretical framework – a hypertheory in the terminology of Wasserman, 1981, or a metatheory serving as the generic core of an interconnected structure of subtheories in the terminology of Tuomi, 1981. (See also Caplan, 1978.) From just the synthetic theory plus suitable boundary conditions, one cannot derive claims about major patterns in the paleontological record, the causes or patterns of speciation, the importance of speciation (in contrast to other factors) in the dynamics of evolution, the evolutionary importance of sex, the evolutionary grounds for alternative life history strategies, and so on. Historically, the synthesis offered a *modus vivendi* that allowed theorists, experimentalists, and field naturalists coming from different disciplines to work together on various problems from within a common framework.

The synthesis was unquestionably of great value. It facilitated the crossing of disciplinary barriers in order to accomplish an immense amount of empirical and theoretical work, with relative freedom from unproductive disagreement over fundamentals and over the value (if not the interpretation) of the available evidence. The gain was a forty-year period within evolutionary biology of something like what Kuhn (1970) calls 'normal science',² allowing a number of evolutionary subdisciplines to develop a firm basis from which to face fundamental evolutionary questions. The dominance of the synthetic theory, however, also allowed certain basic theoretical issues to be set aside before they had been firmly resolved on a satisfactory theoretical or evidential basis.

The books reviewed here are a small and unrepresentative sample of the enormous recent literature attempting to articulate the content of the synthesis, evaluate its historical role, assess its biological merits, and revive some of the alternatives it set aside. Three of them present helpful analyses of issues central to the current controversies over the synthesis. Two of the three tend to suggest that the synthesis has outlived its usefulness as a treaty. The present discussion will seek to evaluate such claims.

First, however, we need a preliminary characterization of the volumes under discussion. Two (Reid and Eldredge) are single-authored. Reid is a comparative physiologist. His *Evolutionary Theory: the Unfinished Synthesis* is thoroughly unsympathetic to the synthetic theory, which he never bothers to define or delimit usefully. Reid is struck by the biochemical conservatism of evolution and concludes from it that "physiological systems must progress by a reorganization of the conservative biochemical units" so that "the key to understanding physiological evolution must be the coordination of interrelated systems" [p. 3]. He believes that such reorganization and coordination cannot be understood solely in terms of, or traced back to, adaptive modification of structural genes. In place of the synthetic theory he advocates a form of emergencies, intended to provide "a means of integrating information on variation and its evolutionary consequences in a holistic manner that is in contrast to the *ad hoc* approach of selections [p. 338]." The book is difficult to read, offers little or no argument and very little evidence favoring this contrast, and mistakes the historical existence of minority points of view concordant with his own concerns for evidence that those concerns deserve to be taken seriously. Its main value is Reid's documentation of the views of precursors, based on extensive study of

² It should be pointed out, however, that there were many ways of doing evolutionary biology and that the advent of molecular biology provided a major alternative style within some evolutionary disciplines. This means that there was not a single "normal science" in evolutionary biology and that biology was not by a single paradigm, as Kuhn's philosophy suggests a mature science should be.

about two hundred years of literature.³ He has amassed considerable information about traditions and approaches not emphasized by historians of Darwinism or by biologists working within Darwinian traditions. Although he provides considerable ammunition for those who wish to develop or understand lines of work not prominent in the synthesis or its Darwinian precursors, his book is of little help to us and will not be discussed further.

Eldredge's *Unfinished Synthesis: Biological Hierarchies and Modern Evolutionary Thought* is a very different sort of volume. Fully one-half of it is devoted to a sympathetic exposition of the seminal books of Dobzhansky (1937 and 1941), Mayr (1942), and Simpson (1944) and, more sketchily, the subsequent development of the synthetic theory. This exposition serves Eldredge's argument that the synthesis is fundamentally incomplete and needs to be completed by a doubly-hierarchical theory (one hierarchy ecological, the other genealogical).

The two collections, Pollard's *Evolutionary Theory: Paths into the Future* (ten chapters, 16 authors) and Ho and Saunders's *Beyond Neo-Darwinism: An Introduction to the New Evolutionary Paradigm* (14 chapters, 16 authors), are edited by biologists seeking to motivate and develop a radical alternative to the synthetic theory. There is considerable overlap between the two volumes, both in themes and in authors. Both books deal with evolutionary issues raised by the complexity of organisms, the internal dynamics of the genome and of ontogeny, cladistics, rational morphological theories of form, the alleged incorporation of environmental information into the genome, epigenetic analyses implicating the involvement of environmental information in development, and the potential contributions of near equilibrium thermodynamics to evolutionary theory. The spectrum of opinions, arguments, and topics presented is well suited to our purpose.

How Should We Interpret the Synthesis?

The synthetic theory of evolution is a moving target. Over its first 25 or 30 years the synthesis hardened, at least to some extent, into unexamined dogma (cf. Gould, 1983, or Eldredge, 1985, p. 100), sometimes dismissing viable alternatives on the basis of prejudgment rather than hard evidence. Our concern, however, is not whether the synthesis became needlessly dogmatic. Working with the issues raised in the books here reviewed, I shall point the discussion to the following questions: To what degree are underlying assumptions of the synthetic theory correct and adequately supported? Does it offer the best means for developing powerful and empirically adequate theories dealing with evolutionary issues like those cited in my first paragraph? Does acceptance of the commitments of the synthesis hide major evolutionary problems or make them more difficult to solve? Are its claims testable, or does the synthesis manifest methodological flaws that inhibit the testing of evolutionary hypotheses or theories?

Eldredge shows (as many others have shown – cf. the epigraph from Mayr) that the synthesis in its early phases was content to establish the *compatibility* of the claim that evolution is primarily driven by natural selection operating on random genetic variation with the findings of all of the sciences dealing with evolution. In this context, the term 'random' has a technical

³ As a sometime historian, I must add word of caution. In spite of the wealth and value of the material that Reid has canvassed, he often does not pay sufficient attention to the problem context and intellectual setting within which his protagonists were working. In consequence, he often treats them as speaking more directly to each other and to issues of current concern than he should. For those who are interested in the historical material, Bowler (1983 and 1984) covers a good deal of the same ground in a more satisfactory and reliable way.

meaning – to wit, *not oriented by or with respect to the requirements of phenotypic adaptation*. As we shall see, even now this concept is seriously misunderstood by many critics of the synthetic theory.

Part of what is meant by calling the synthesis a treaty or a metatheory is that, in its concern to establish the *compatibility* of the standard population genetic accounts of microevolution with all known evolutionary (especially macroevolutionary) phenomena, it disarmed conflicts between disciplines bearing on evolutionary history. By itself, population genetics was unable to make powerful predictions about large-scale evolutionary phenomena. Thus, claims about the general patterns of evolution were drawn from other disciplines,⁴ but, on the basis of extrapolation of the *mechanisms* taken into account in population genetics, it became reasonable to suppose that there was no conflict between population genetics and the historical patterns revealed by paleontology, the contemporary structure of the Linnaean hierarchy, the findings of ecology regarding the consequences of competition or symbiosis, and so on. To this extent Stebbins and Ayala (1981) are correct when they argue, for example, that the genetic arguments supporting microevolutionary gradualism are compatible not only with phyletic gradualism but also with fairly extreme versions of the punctuated equilibrium hypothesis regarding the pattern of the fossil record. Although many proponents of the synthetic theory were, indeed, committed to the predominance of gradual phyletic evolution, that position seems independent of the remaining commitments of the synthetic theory.

During the early days, the very weakness of this compatibility claim was viewed as one of the *strengths* of the synthesis. In principle, virtually all of the known phenomena and patterns that ought to be explained by an evolutionary theory *could* be explained by the synthetic theory – and so it was not necessary to contemplate or turn to any rival theories. As the synthesis hardened, 'could be explained' turned into 'are explained', yielding outright dismissal of competing theories. To some this seemed to turn the synthetic theory into an *a priori* rather than an empirical doctrine.

In spite of how it may have seemed, however, the synthetic theory is no tautology, Riddiford and Penny point out in their nicely balanced opening chapter of Pollard,⁵ Far from being true *a priori*, it *is* testable, for it is not compatible with all possible phenomena.⁶ Nonetheless, there is considerable difficulty in getting a precise fix on the testable content of the synthetic theory (measurable by the list of phenomena with which it is incompatible), in delimiting its explanatory power, and in specifying its precise commitments. This makes it

⁴ Mayr has been, perhaps, the most vocal advocate of contributions by non-geneticists to the synthesis. Eldredge (pp. 43-44) abstracts Mayr's (1980) list of the contributions of systematics to the synthesis as follows: "(1) 'population thinking,' (2) 'the immense variability of populations,' (3) 'the gradualness of evolution,' (4) 'the genetic nature of gradual evolution,' (5) 'geographic speciation,' (6) 'the adaptive nature of observed variation,' (7) 'belief in the importance of natural selection,' and (8) the notion (shared with paleontologists) that 'macroevolutionary phenomena' are interpretable in terms of 'gradual evolution' (i.e., as opposed to saltational models)." Whatever one thinks about the details of this list, it illustrates some of the fundamental programmatic commitments of the synthesis and shows how much room there was within the treaty for developing substantive models for application to particular evolutionary processes.

⁵ This chapter, "The Scientific Status of Modern Evolutionary Theory," and the next, Philippe Janvier's "Cladistics: Theory, Purpose and Evolutionary Implications" provide excellent reviews, suitable for use in upperclass courses.

⁶ They cite an example due to Maynard Smith: if some deep sea fish carried a variable number of luminous dots on their tails, but the numbers were always prime numbers, one would have to abandon the synthetic theory. But Darwin himself had already made a similar point: "If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection" [Darwin, 1859, p. 201].

understandable that its opponents typically offer contradictory criticisms of the theory, e.g., sometimes arguing that it is deficient because it can explain everything (shown to be incorrect in n. 6) and sometimes that it can explain nothing (e.g., because its central principles are tautologous, which is equally incorrect). All too often, however, the critics' version of the synthesis is a straw man.

The Pollard and the Ho and Saunders volumes include quite a few attacks on such a straw man. Many of the papers exhibit serious confusion about which of their own claims are compatible with the synthetic theory. The following sections, devoted to three of the central themes raised in these volumes and in Eldredge, show that, far too often, the critics' general stance is seriously undermined by their misinterpretations of the synthesis.

Biased Variation, Internal Dynamics, and Evolutionary Conservatism

Sidney Fox, writing on "Proteinoid Experiments and Evolutionary Theory" in Ho and Saunders, strikingly exemplifies the pernicious confusion regarding random variation. Darwin claimed only that variation is copious, predominantly small, and available in virtually any [gross phenotypic] direction from the normal condition.⁷ Few of the major theorists of the synthesis claimed (or would have claimed) that variation *of all sorts* is randomly distributed about the initial state of a population. Rather, they claimed that no process is available to orient variation with respect to the current or future adaptive needs of the organisms comprising populations. This accorded well with their zoologically biased Weismannian conviction that germ line nuclei are protected from somatic influences and their allied rejection of neo-Lamarckism. Here is what Fox says:

We ... have two principal definitions of random, as well as shaded definitions in between. In one definition, random means random, as now statistically defined. In the other, it means essentially undirected. [Note: this *should* read *undirected with respect to the adaptive requirements of the organism* – RB.] A principal thesis of this chapter is that variations are directed, and that they are directed from the molecular level within an hierarchical organization (p. 19).

Fox's striking experiments, summarized in part in this chapter, show that the molecules relevant to protobiological processes exhibit preferential relationships (e.g., that amino acids tend to self-sequence in protocells). Accordingly, he concludes from protobiological results that "the neo-Darwinian formulation of evolution as the natural selection of random variations should be modified ... to the *natural selection of non-random variants resulting from synthesis of proteins and assemblies thereof*" (p. 16).

Fox deals with protoevolution. Others (e.g., Løvtrup and Saunders in Ho and Saunders) deal with development, arguing in parallel fashion that natural selection acts on non-randomly distributed variation. But *insofar as they do not demonstrate that the adaptive requirements of organisms affect the distribution of variation, their claims are compatible with the framework of the synthesis*. In most of the chapters the relationship between claims about biased variation and the position of the synthesis with regard to variation is glossed over without proper attention to these issues. The inevitable result is confusion.

⁷ The logic of Darwin's support for gradualism turns on this characterization of available variation. Cf., e.g., Darwin, 1859, pp. 466 ff. where he argues explicitly that "natural selection acts solely by accumulating slight, successive, favorable variations" and that "nature is prodigal in variety, though niggard in innovation" [p. 471].

It remains true, of course, that biased variation raises serious problems for the synthetic theory. Natural selection, notoriously, can act only on available variation. From Darwin on, major theorists have stressed that evolution by natural selection is a two-step process. Variation is produced in one step. In a second, independent, step certain variants are brought to prevail (or not) over alternatives in the population by selection. This leaves a major problem open: how significantly do the limitations on available variation constrain the course of evolution? Darwin clearly recognized the inadequacy of the then available knowledge of the causes and limitations of variation. He thought, however, that variation is sufficiently copious that virtually any reasonable physically realizable phenotypic modification could be achieved in the course of geological time. *But what should count as reasonable?* The question is a tricky one. Both Darwin and the theorists of the synthesis⁸ suggest that it could be answered in due course by the "normal scientific" acquisition of knowledge about the character, causes, and availability of variation. And both recognized that the contribution of biased variation to the course of evolution is an open problem.⁹

Recently, theoretical and evidential considerations have led to wide recognition that the rate of morphological evolution does not correlate directly with the gross rate of molecular evolution and that molecular evolution, itself, proceeds at very different rates for different molecules produced under genetic control and in different compartments of the genome. The relevant considerations are drawn from many sources, including the paleontological data used to support the theory of punctuated equilibrium,¹⁰ a variety of arguments based on new knowledge of the epigenetic mechanisms involved in ontogeny,¹¹ arguments for the genomic acquisition of environmental information,¹² and a mixture of theoretical and empirical studies of the rates and molecular mechanisms of genomic change.¹³ It has come to be widely accepted that in at least some cases the internal dynamics of biased variation contributes to molecular evolution (and perhaps to evolution at higher levels)¹⁴ and, more controversially, that such phenomena and the mechanisms allied with them may have something to do both with evolutionary trends and with

⁸ This issue was seldom in the foreground. Nonetheless, it is obvious that some variants – e.g., the evolution of metal skins – would be ruled out of court by all Darwinians on grounds that no pathway of variation was available by means of which to achieve such an end state even if that state were adaptively satisfactory.

⁹ It must be confessed that for many adherents of the synthesis, Fisher's demonstration that even weak selection could overcome rather extreme mutation pressure seemed to resolve this problem. This is, however, simply a mistake since the result says nothing about how selection could achieve phenotypes which are unavailable due to the absence of appropriate variation.

¹⁰ Such data is not directly discussed in the works reviewed here, but both Eldredge in his book and E. Vrba in Ho and Saunders ("Patterns in the Fossil Record and Evolutionary Processes") discuss the punctuational pattern and provide some references to the abundant literature on the topic.

¹¹ Discussed by Løvtrup ("Ontogeny and Phylogeny"), B. Goodwin ("A Relational or Field Theory of Reproduction and its Evolutionary Implications"), and Saunders ("Development and Evolution") in Ho and Saunders and by Goodwin ("Changing from an Evolutionary to a Generative Paradigm in Biology") in Pollard. These articles are, of course, a very small sample of a very large literature.

¹² Cf. for example Ho ("Environment and Heredity in Development and Evolution") and Pollard ("Is Weismann's Barrier Absolute") in Ho and Saunders and C. Cullis ("Environmentally Induced DNA Changes") and E. Steele et al. ("The Somatic Selection of Acquired Characters") in Pollard. The latter work is highly controversial.

¹³ Considerations based on such work are central to Pollard ("Is Weismann's Barrier Absolute?") in Ho and Saunders and to H. Temin and W. Engels ("Movable Genetic Elements and Evolution"), and the Cullis and Steele et al. articles in Pollard.

¹⁴ For one example, the P elements in *Drosophila*, discussed briefly by Temin and Engels at p. 179ff. in Pollard, spread horizontally within the germ line and are likely candidates for causing speciation because they yield hybrid dysgenesis in crosses between lines with and lines without P elements.

the paleontologists' findings of an unexpectedly high degree of morphological conservatism within lineages. The latter suggestion, though not supported by hard evidence, has been welcomed by some proponents of the punctuated equilibrium hypothesis.

These findings and various allied theories raise difficulties for the synthesis, difficulties that tend to elicit one of two characteristic responses. The first attempts to *extend* the synthesis by filling in missing knowledge (e.g., about the causes and evolutionary importance of biased variation) without altering its fundamental commitments. The second, often based on the belief that some of the putative genomic and cellular mechanisms contributing to biased variation provide a fundamental alternative to random variation plus natural selection, seeks to replace the synthesis with an alternative theory or research program. The difficulty in choosing between these responses is considerably exacerbated by the confusion already illustrated over the proper content of the synthesis. Many of our authors suffer from this confusion. With the exception of Eldredge, they tend, however, to favor the second option.

Hierarchy

A second source of difficulty for the synthesis concerns the importance of the hierarchical structuring of biological entities in producing evolutionary patterns. The most systematic discussion of hierarchies in the volumes here reviewed is found in chapters five through seven of Eldredge. I shall concentrate here on his approach to the issues raised by the importance of biological hierarchies as causes of evolutionary patterns.

Let me start with an extremely compressed summary of the principal argument for the existence of higher-level units of selection. The argument rests on an analogy. (Sexual) organisms form (interbreeding) populations; mutation and available variation among the members, plus differential rates of survival and reproduction, lead to shifts in the features of the organisms (and of distributions of features within the population) over time. Natural selection as usually conceived is the systematically biased redistribution of traits in populations of descendant organisms due to whatever sorts of advantages are provided by particular parental traits.

And now the analogy: various higher level entities (e.g., demes and species) are historical units analogous to organisms. These units differ from each other within the larger cadres that contain them and manifest differential rates of survival and reproduction (here deme formation or cladogenesis), leading to shifts of modal features in the species or larger clade. Deme or species selection is the systematically biased redistribution of features in descendant cadres caused by the traits of particular demes (e.g., a propensity to send out propagates at lower or higher density) or species (e.g., being composed of organisms that reproduce sexually vs. asexually). Insofar as the traits of the demes or species in question are not straightforward sums of the properties of the component organisms or demes, such putative higher level selection cannot be reduced to organismal (in some usages 'natural') selection. The argument for lower-level (e.g., genic) selection is exactly parallel. Strings of DNA, for example, are historical entities forming populations. They reproduce with considerable, but not perfect, fidelity and leave descendants. The distribution of features (e.g., nucleotide sequence) in the populations of descendants is systematically biased in consequence of the advantages enjoyed by their 'parents' in either surviving or replicating (making copies). It should be obvious that these advantages turn in part on the company kept by the parent strings – e.g., the other strings of DNA with

which they are associated – and on the features and circumstances of the organisms in which they are found. Thus, formally speaking, similar stories about selection can be told at many levels.¹⁵ (It is perhaps worth noting explicitly that hierarchical structure enters into the stories at all of the levels.) The levels themselves form some sort of inclusive hierarchy – a hierarchy that includes at least genes, portions of chromosomes, organisms, demes, species and monophyletic taxa. The unifying nexus at each level (except, perhaps, that of monophyletic taxa) is reproduction and the resultant genealogical tree provides the footing for the entry of selection into the story.

None of our authors is sufficiently careful about the various meanings of 'hierarchy'. Grene, 1987, divides hierarchies into two major types. One consists of 'control hierarchies', in which information (and, I would add, matter and energy) flows between entities at different levels, yielding constraints – typically *both from above and from below* – on the behavior and fate of the entities at a given hierarchical level. The other sort consists of classificatory hierarchies, which include and are like the Linnaean hierarchy in that they are unidirectional and not dynamic. Although no such distinctions are developed by our authors, they do raise the central issues clearly enough: do [control] hierarchies of various sorts play a causal role in evolutionary history, affecting or effecting major evolutionary patterns? Need we take account of hierarchical structures (e.g., of epigenetic developmental programs, or of nested taxa such as demes, species, and monophyletic taxa) in order to portray evolutionary dynamics correctly? If so, must we complicate our account of natural selection and 'random' variation in ways that break the mold of the synthetic theory?

At this point we turn to Eldredge. Building on slightly variant distinctions between 'replicators' and 'interactors' (Hull, 1980) or 'replicators' and 'vehicles' (Dawkins, 1976, 1982; see also Brandon, 1985), Eldredge argues that we must distinguish between two distinct hierarchies, one genealogical and the other ecological. The distinction rests on the 'glue' that unifies the relevant entities in each hierarchy – reproduction or replication ('more making') in the case of the genealogical hierarchy and unitary participation in the 'economics' of making a living (the transfer of matter and energy) in the case of the ecological hierarchy.

I read Eldredge as making two major claims about these hierarchies. (1) With the exception of organisms, they involve distinct entities. (By and large, it is not in virtue of the direct interactions of genes, demes, and species with one another or with the environment that they replicate differentially, and so they do not belong in the ecological hierarchy. Enzymes, somatic cells, regional biota, and local ecosystems do not reproduce or replicate in the relevant trans-generational sense, and so do not belong in the genealogical hierarchy. Organisms both interact and reproduce and *do* belong in both hierarchies.) (2) To understand selection at any level, one must distinguish between the reproductive nexus and the interactive nexus. Reproduction, alternatively replication, is, ultimately, the principal source of the phenotypic variation on which selection acts; reproduction provides essential raw material from which the interacting entities are formed and it provides the variants that must be counted to determine whether or not systematic statistical biases of the sort that constitute natural selection have occurred. (But see Brandon, 1985, for an argument that the statistical biases are nonetheless caused at the level of the interactors so that, if one employs the metaphor of selection *acting*, selection acts on interactors, i.e., in the standard case it acts at the level of the organismic

¹⁵ The *locus classicus* for the conditions under which, when satisfied, yield an account in terms of selection is Lewontin (1970). A useful compilation of articles regarding units and levels of selection is Brandon and Burian (1984).

phenotype.) The fate of interactors determines survival of replicators and has enormous influence on differential reproduction. (For example, interacting populations are composed of demes; the interactions of the populations greatly affect the survival of various demes whose continuation and production of new demes supplies the raw material for the continuing interactions between populations.) The entities at various levels that interact with one another are usually different than the ones that replicate or reproduce. To the extent that traditional evolutionary theories – including the synthetic theory – fail to recognize this, they risk serious mistakes in their treatments of particular cases. This analysis clarifies and strengthens the long-standing claim that evolution by means of natural selection is a two-step process, for variation in the genealogical hierarchy usually concerns different entities than those on which selection acts.¹⁶

What is the impact of such claims on the synthetic theory? Eldredge suggests that all of the elements of his own account were put forward in the founding documents of the synthetic theory, especially Dobzhansky (1937), and that his hierarchical theory should be interpreted as an extension of the synthetic theory in directions that it implicitly allowed from the beginning but that were to some extent foreclosed by the hardening of the synthesis – especially its restriction of natural selection to the focal level of organisms and its insistence that the predominant source of evolutionary pattern is adaptive evolution conceived in terms of natural selection acting only at the level of organisms.

Thus, even though he is a proponent of stasis and punctuation as the dominant evolutionary pattern and, to that extent, an opponent of the most simple-minded (and incorrect!) conventional gradualist extrapolation of microevolutionary patterns, he does not believe that he has undermined the synthetic theory's characterization of the evolutionary process – at least not unless that characterization is interpreted so as to exclude selection acting at other hierarchical levels than those of gene or genome (as replicator) and organism (as interactor). Rather, he claims to have expanded the synthesis by explicitly recognizing the hierarchical complexity of differential interaction and reproduction. This recognition means that the theorist does not have to explain virtually all evolutionary phenomena as arising either from 'neutral' variation or from selection *operating at a single focal level*. It thus expands the recognized sources of evolutionary pattern, increases the resources available for use in explaining particular evolutionary histories, and reduces the emphasis on *organismic* adaptation since at least some organismic evolution is a byproduct of processes occurring at other levels. All that is involved is an extension of the list of mechanisms already taken into account by the synthetic theory. (Somewhat similar views, embedded in an argument that they constitute a rather stronger departure from the synthetic theory, are offered in Gould, 1982.)

A number of our other authors disagree sharply with Eldredge at just this point. Many of them seek to develop radical alternatives to the synthetic theory and are, therefore, inclined to interpret it as incompatible with biased variation, with hierarchically structured mechanisms affecting evolutionary pattern, and so on. Both the Pollard and the Ho and Saunders volumes contain numerous proclamations of the insufficiency of the synthetic theory and claims that we

¹⁶ One word of caution: where differential replication below the organismal level is a result of the 'phenotypes' of the replicators themselves (as is the case, I claim, with certain transposable elements and many categories of 'selfish DNA'), selection also 'acts' directly at the level of replicators – i.e., *there are systematic statistical biases as between alternative replicators in virtue of their intrinsic properties rather than in virtue of a cascade of consequences that those properties have on entities at different levels.*

are witnessing the end of its dominance in evolutionary biology.¹⁷ These claims, I think, are largely misguided, not only because they uncharitably or confusedly misconstrue the synthetic theory, but also because of mistaken presuppositions about what an evolutionary theory should be and do. That will be the topic of the next section, after which we will return to the question of the present status of the synthetic theory.

Unifying Theories

Physics envy has long been the curse of biology. This curse often expresses itself in the desire for a grand unifying theory with the predictive and explanatory virtues and the testability of Newtonian mechanics. A number of our authors (e.g., Brooks and Wiley, Fox, Matsuno, and Wicken explicitly, and Goodwin, Ho and Saunders, Løvtrup, Pollard, Rosen, and Webster implicitly) seek such a strong theory to serve as the core of evolutionary biology. They are right that the synthetic theory does not fit the bill, but it is not obvious that they can reasonably expect some other theory to do so. My discussion of this issue will emphasize, and draw some consequences from, the historical character of evolutionary biology. I am particularly interested in finding out what sorts of theories one can reasonably expect to find at the center of the discipline.

The synthetic theory, like Darwinism generally, claims that the details and many of the basic patterns of organismic evolution are, at heart, historically contingent. On Gould's persuasive account, Darwin's central accomplishment in this regard was to build a theory that accounted for taxonomic and morphological order in terms of "historical pathway, pure and simple," rather than in terms of "intrinsic purpose and meaning" [Gould, 1986, p. 60] or of laws of form. For Darwinians, homology is explained by common descent, whereas similarity of functional form (analogy), however striking, is accounted for by the adaptive power of selection.¹⁸

We recognize the occurrence of evolution and delineate phylogenies in part by means of the 'accidents of history'. The term is apt. Cladistics, "the science of ordering by genealogical connection, *and nothing else*" [Gould, 1986, p. 66], does much of its work by ascertaining which organisms or taxa share common derived characters ('synapomorphies', cf. Janvier in Pollard, pp.

¹⁷ For example Saunders, at pp. 255-256 of Ho and Saunders, argues that development is characterized by homeorhesis (staying within one valley of Waddington's 'epigenetic landscape' through a considerable range of perturbations) and heterorhesis (sudden switching from one such valley to another, resulting in a large organized change of phenotype). He portrays heterorhesis as a way of reconciling evolutionary theory with the fossil record, believing falsely that the only way a synthetic theorist can explain the gaps in the fossil record "(apart from a flat denial that real gaps exist) appears to be to postulate mutations in regulatory genes" [p. 256]. Ironically, the theory of punctuated equilibria was originally propounded by Gould and Eldredge as a projection onto the fossil record of the consequences of Mayr's peripatric and allopatric models of speciation (Gould, 1982, p. 383). The epigenetic account may in the long run prove correct, but the false estimate of the resources and commitments of the synthetic theory is a cheap and impermanent way of purchasing victory over it.

¹⁸ Cf. Darwin, 1859, p. 206: "It is generally acknowledged that all organic beings have been formed on two great laws – Unity of Type and the Conditions of Existence. By unity of type is meant that fundamental agreement in structure, which we see in organic beings of the same class, and which is quite independent of their habits of life. On my theory, unity of type is explained by unity of descent. ... [N]atural selection acts by either now adapting the varying parts of each being to its organic and inorganic conditions of life; or by having adapted them during long-past periods of time; ... Hence, in fact, the law of the Conditions of Existence is the higher law; as it includes, through the inheritance of former adaptations, that of Unity of Type." [Also cited at n. 37 of Gould, 1982.]

42 ff.). While our assessments of particular traits as synapomorphies may be mistaken, there can be little doubt that cladistic methodology is fundamentally sound. To that extent, we have an argument against the derivation of basic evolutionary patterns from the laws or axioms of evolutionary theory.

Compare, for example, biological with stellar evolution. In the latter case, each star has unique properties and, typically, is formed from material that once belonged to previous stars. Nonetheless, parentage is irrelevant to the behavior and to the fate of a star (and to the patterns of behavior of populations of stars). The main properties of stars can be derived from initial conditions and fundamental physical laws. Barring highly unusual interactions with other cosmic bodies, each stage in the history of a star can be derived from its intrinsic properties (mass and composition) and appropriate initial or boundary conditions (relative positions and velocities of its constituents and any relevant neighboring objects). 'Accidental' properties like those relevant to evolutionary study of biological entities are irrelevant to determining the parentage and behavior of stars, their likely fate, or the patterns of evolution of populations of stars. In part this is because stars are sufficiently isolated that the dominant determinants of their behavior, once certain initial conditions have been realized, are fundamental physical laws.

There are good reasons for supposing that the same is not true for organisms. If the laws of thermodynamics, for example, were powerful enough to determine the patterns of evolutionary history in detail, the evolutionist's use of 'accidental' clues would amount to a deep mistake; instead of supplying crucial information bearing on the behavior and fate of organisms (or other biological entities), it would mask the fundamentally law-driven course of evolution. If laws of form determined ontogenies rigidly, organisms, like stars, would simply have one or another of the available ontogenies and the transition from one ontogeny to another within a lineage would not be marked by any clues about the history of the lineage. But organisms and lineages *do* record the accidents of history. (The gill slits of mammalian embryos suffice to make the point.) In the end, both cladistics and evolutionary biology as a whole depend deeply on the contingent fact of evolutionary tinkering (Jacob, 1982).

Insofar as evolutionary theory is concerned with analyzing genealogical connections or patterns of genealogical affinity among organisms (and biological entities at other levels, such as DNAs and species), it cannot escape the essential historicity of biological evolution. The same applies when the concern is to develop 'laws' governing or describing patterns of evolution among DNAs, proteins, organisms, taxa, or clades. Nor can one escape this historicity by turning to a generalized mechanics for evolution. Two examples illustrate the point. (1) The effects of particular molecular mechanisms – and even the content of the genetic code itself – are highly context dependent. Thus whether a given string of DNA will yield or affect the expression of a particular product depends on the cellular and genetic context within which it is placed. There is no prospect of a generalized mechanics of gene expression powerful enough to take all of the contextually relevant factors into account (except, perhaps, statistically). That is why the analysis of gene expression is a brute force, messy problem rather than a neat theoretical enterprise. (2) Speciation depends in part on such matters as mate recognition which, in turn, depends on the use of 'accidental' characters *by the organisms themselves*. (Cf., for example, Eldredge's discussion, pp. 156 ff., of Paterson's account of Specific Mate Recognition Systems, developed, e.g., in Paterson, 1982.)

This historical component of the Darwinian explanation of underlying form has often been overlooked. It undermines the arguments of those who sought to prove that the synthetic theory meets the tough but inappropriate methodological strictures of Popper and others whose

philosophies of science are based on an analysis of theoretical physics or who sought to develop an alternative theory meeting those strictures. The point is not that claims regarding evolutionary pattern or phylogenies are untestable – on the contrary.¹⁹ Rather, it is that the basic principles of historical theories do not play the same role or have the same character as the basic laws of mechanics or other 'ahistorical' theories.

A historical theory may (perhaps must) presuppose as background ahistorical laws which, if correct, provide the constraints²⁰ within which history runs its course. Nonetheless its principles must provide the basis for an account of the causal relevance and relative importance of multiple processes, patterns, and singularities whose historical roles are not wholly determined by those laws. Those principles must allow alternative models and smaller scale theories to be applied to particular cases. This is part of what Wasserman (1981) means when he calls evolutionary theory a hypertheory and Tuomi (1981) means when he calls it a metatheory – the principal work of prediction and explanation is done by models or subtheories less general than the theory of evolution, but compatible with its principles. To this extent those principles cannot be expected to yield rigorous deductions of specific outcomes (even when appropriate boundary conditions are supplied) – although those outcomes *could* be derived from first principles plus boundary conditions *if only one causal process (or a small number of causal processes in a fixed relationship) were involved*.

Thus the role of laws and general principles in evolutionary explanations is not the same as it is in the standard theories of physics. They set the frame within which specific explanations are to be constructed and give guidance about that construction, but they do not provide the wherewithal for a full derivation, even when supplemented with appropriate boundary or initial conditions. This may be the reason for the seemingly inconclusive character of many debates over the dominant historical patterns in evolution (e.g., gradualism vs. punctuation) and the mechanisms underlying those patterns (e.g., the causes of trends, the relative importance of selection and drift, the debates over the units of selection and the relevance of hierarchical structure). In all of these cases we are dealing with questions of relative frequency. In all of these cases, examples can be found that support the existence of whichever pattern in question or the efficacy of whichever mechanism. In all of these cases, the patterns and mechanisms are compatible with the leading principles of the synthetic theory *provided that those principles are stated abstractly enough*.²¹ Nonetheless, the alternative scenarios involve *specifications* of those

¹⁹ Molecular techniques now make detection of homology a straightforward task, though one requiring brute force. Gould puts the point neatly: "The recovery of homology only requires a source of information with two properties: sufficiently numerous and sufficiently independent items to preclude, on grounds of mathematical probability alone, any independent origin in two separate lineages. The 'items' of morphology are too few and too bound in complex webs of developmental correlation to yield the required independence. Yet the discoveries and techniques of molecular biology have now provided an appropriate source for recovering homology – a lovely example of science at its unified best, as a profession firmly in the camp of repetition and experiment provides singular data for history. Molecular phylogenies work not because DNA is 'better,' more real, or more basic than morphology, but simply because the items of a DNA program are sufficiently numerous and independent to ensure that degrees of simple matching accurately measure homology." [Gould, 1986, p. 68].

²⁰ These constraints are 'universal constraints' (as contrasted with 'local constraints', which are historical in character) in the terminology of Maynard Smith et al., (1985). This article provides a useful review of the status of constraints in current evolutionary theory.

²¹ One important aspect of debates over group selection, hinted at in n. 15, is that the conditions set forth in Lewontin (1970), widely accepted in the literature as sufficient for the occurrence of a selective process, can in principle be applied as readily to strings of DNA, demes, groups of various sorts, and species as they can be to

principles that depart in varying degrees from the spirit and content of the beliefs of the founders of the evolutionary synthesis. To this extent, even though (as I have argued) no suitable radical alternative is in sight, the fate of the synthesis *as a coherent system of beliefs* is very much up in the air.

An Optimistic Conclusion

The position at which we have arrived may appear extremely pessimistic to some readers. It is important to counteract this appearance. I have argued that evolutionary biology is, unavoidably, an historical discipline. As such, it is unreasonable to expect the field to be based on a theory whose core consists solely of ahistorical (time symmetrical) laws. (The specific content of the genetic code and, probably, the unique role of DNA in cellular organisms are contingent states of affairs that surely must be understood in terms of history in the sense that these outcomes are not simply the necessary consequences of evolutionary laws applied to some class of carbon-rich planets that maintain, for a certain extended interval, a certain amount of surface water and a fairly temperate regime.) I have also argued that even though current evolutionary theory is not a predictive theory in the style of Newtonian mechanics or its current successors, the claims of evolutionary theory (and lower level claims assessing, e.g., particular phylogenies or the relative frequency of particular evolutionary patterns) are testable. In this brief concluding section I shall speak optimistically of the prospect of expanding the tests of evolutionary theory and of resolving some of the central issues that have plagued it. I will then close with a summary statement on the current status of the synthetic theory.

As was pointed out in n. 20, the development of sequencing techniques has opened up new possibilities for assessing homology – i.e., of determining whether similarity of characters is due to common descent. The independence of amino acid sequences in different proteins (or nucleotide sequences in different DNAs) within a single organism (a matter itself subject to test), plus the (contested) evidence for fairly regular rates of amino acid or nucleotide substitution in particular molecules or parts of molecules, means that an astronomical number of scorable and datable independent characters are available for brute force assessment of similarity. This, in turn, allows rigorous testing of hypothesized phylogenies. In fact, work along these lines has produced highly concordant phylogenetic trees – the concordance itself serving to support the scheme – trees which have been established, virtually for the first time, without any reliance on morphological similarities. As a result it is possible to compare rates of morphological evolution with rates of phylogenetic and molecular change. This provides a new footing for assessing the place, importance, and target of natural selection in evolutionary history.

The problem of determining the 'inertial baseline' (a term that both Elliott Sober and I have used) from which selection departs – e.g., of determining what would happen to relevant sorts of complex genetic and biochemical systems, once they were up and running, in the absence of selection – also looks somewhat more tractable than before. One line of work not yet mentioned, opened up most notably by Kauffman, e.g., 1985 and 1993, suggests that it is possible to evaluate the statistical features of very general classes of genetic systems so as to reveal important ensemble properties that would be manifested by genomes and proteins *in the absence of selection*. If this can be done, whether with Kauffman's protocols or with others

organisms. Thus whether selection in a particular case occurs at a one or another level – say at the level of organisms or of demes – is not settled by formal, but by factual considerations.

currently being developed, it will be possible greatly to improve our estimates of the contribution of selection to the present genomic structures of organisms and the extent to which the same structures should have been expected in the absence of selection. Other lines of work, mentioned in passing above, provide improved means of estimating biases in genomic variation on grounds of our rapidly increasing mechanistic knowledge of DNA and chromosomal mechanics. This, too, opens up improved means of estimating the extent to which particular patterns are caused by biased variation and the extent to which they are caused by selection. Similarly for estimating the importance of neutral variation. In short, the use of a variety of new techniques promises to provide new data and new theoretical toeholds for evaluating the relative preponderance and importance of alternative modes and patterns of evolution. Whether this will allow us to resolve some of the long-standing issues that have been set aside or that have exceeded the power of hitherto-available techniques I am not sure, but there are plenty of avenues to explore.

From a very different perspective, work on hierarchy seems to justify similar optimism. The gradual clarification of the issues surrounding the hierarchical structure of biological entities, the conditions that must be met by 'higher level' entities if they are to play a genuine causal role in shaping evolutionary history or bringing about evolutionary patterns has pointed us toward a variety of empirical questions susceptible of serious test. To what extent do (sub)clades exhibit differential survival or cladogenesis when subjected to ecological or global catastrophe? Do such catastrophes play a major role as precursors of 'adaptive radiations'? Can the differences in rates of cladogenesis or survival be explained wholly by reference to organismic properties (cf. Vrba's 'effect hypothesis', discussed in Eldredge, pp. 132-133, or by Vrba in Ho and Saunders, pp. 128 ff.)? The increased clarity of these questions has gone hand in hand with the development of techniques increasing the strength and reliability of the evidence brought to bear on these questions. Similar claims can be supported for the improvement in the analysis of the putative correlations between constraints operating on developmental systems and the major macroevolutionary steps and 'bridgeless gaps' (the term stems from Goldschmidt) evident in both the fossil record and among contemporary organisms.

In summary, then, the challenges to the synthesis have reopened a large number of fundamental questions about evolutionary patterns and mechanisms. Of these, two seem most critical: (1) the extent to which the molecular inertial baseline – i.e., molecular mechanisms of one sort or another, often categorized, inadequately, in terms of biased variation and neutral mutation – is by itself sufficient to cause evolutionary patterns and the degree to which that molecular baseline is under the control of conventional natural selection, and (2) the extent to which the hierarchical structuring of biological entities vitiates the claim that the natural selection *operating on organismic phenotypes* (especially if these are restricted to adult phenotypes) is the fundamental source of evolutionary pattern. The pursuit of these questions has undermined some of our naive confidence that the classical account of evolutionary pattern as deriving almost wholly from adaptively undirected genetic variation plus differential survival and reproduction *among organisms*.

On the other hand, the synthetic theory can be straightforwardly extended to include biased variation and selective processes at a number of hierarchical levels. Those critics are wrong who maintain that the synthetic theory excludes the recognition of such factors by its very structure. Their inclusion, to be sure, results in a more complicated picture which, when compared with hardened versions of the synthetic theory, allows much less confidence that arbitrarily chosen traits will turn out to be adaptations and, more generally, ascribes reduced importance to differential survival and reproduction *of organisms* as a major determinant of

evolutionary patterns. Nonetheless, no structural feature of the synthetic theory precludes such an extension or places obstacles in the way of the serious pursuit of these problems.

So far as I can see, none of the challenges to the synthesis has yet put forward the sort of alternative that might lead to its abandonment. Such an alternative must be an historical theory or metatheory able to encompass the contingencies of evolutionary history and to place adaptive evolution and selective processes *at all relevant levels* into its account of the genesis of evolutionary pattern. And such an alternative must be based on principles (comparable in scope to the principles of the synthetic theory) that can be used to guide the construction of lower-level theories and models capable of accounting for the occurrence and preponderance of evolutionary patterns. The attempt to produce such an alternative theory is extremely difficult, but surely worthwhile. Though its prospects of success are uncertain it will, no matter what, force us to reexamine our assumptions and the strength of the support for our claims about the causes of evolutionary processes.

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