

5. The Influence of the Evolutionary Paradigm¹

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The central concern of this essay is the relationship between the synthetic theory of evolution and neighboring sciences. In writing about “the evolutionary paradigm” (a title suggested by Max Hecht), I hope to play the role of a philosophical gadfly. In particular, I shall argue that, in one of the most important ways in which philosophers and scientists use the term ‘paradigm’ these days, *there is no evolutionary paradigm* – and hence no influence of ‘the’ evolutionary paradigm.

Obviously I do not mean to suggest that Darwinism has been without influence. Rather, I wish to probe the way we think about the practice and the unity of evolutionary theory and evolutionary biology in general. I will suggest that the muddy concept of a paradigm, as commonly used these days, is one that we can do quite well without, thank you very much. I suggest that bypassing that concept will help us to focus more clear-headedly on the influence of the current variant of Darwin’s theory: the so-called synthetic theory of evolution.

Given the special interest of this symposium in assessing the directions in which evolutionary biology is headed, I will emphasize a characteristic of evolutionary theory which I think is of great importance in thinking about its future: namely, its peculiarly *historical* character. I claim that a full appreciation of the nature of historical theories, historical reasoning, and their role in evolutionary biology ought to shape much of our thinking about the relation of evolutionary biology to other branches of biology and to the sciences more generally. What I have to say about that topic is not particularly original. A good bit of it has been said quite eloquently by Gould and others. But it is definitely worth trying to make it stick, for, as I hope to show, there is a moral of deep interest to be drawn from Darwinism, a moral that yields some strong suggestions about the directions open to evolutionary theory as we come once again, as we do in every generation, to a major crossroads.

About Paradigms

Although I will pay some attention to the term ‘paradigm’, my principal concern is not semantic, but with the social and intellectual structure of evolutionary biology. The point of interest can be put in terms of an evolutionary analogy. A species is composed of many variant individuals, often conveniently grouped into varieties. Similarly, there are many varieties of evolutionary biology and many variant positions within each variety.

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Just as the evolution of species depends on the underlying variation of the individuals of which it is composed, so the development of evolutionary biology depends on the underlying variation among evolutionary biologists. To this extent, it is as worthwhile to ask after the unity in the diversity of evolutionary biology as it is to ask after the unity in the diversity of biological species. The point of worrying about paradigms is to show that some common views regarding the unity of evolutionary biology are not true. Please bear with me, therefore, while I start by clearing some terminological underbrush.

The use of the term ‘paradigm’ in history and philosophy of science traces back primarily to Thomas Kuhn’s *Structure of Scientific Revolutions* (Kuhn 1962, 1970b). There is a large literature discussing Kuhn’s notion of a paradigm. It has been pointed out repeatedly that the term is multiply ambiguous (Masterman 1970). Kuhn himself now admits this and has introduced some new terminology in an attempt to recapture what he takes to be the two fundamental points he was making about the character of major scientific theories and research programs (cf. Kuhn 1970a, pp. 271 ff., and the fuller treatment in Kuhn 1974). The two points are, in fact, fairly straightforward and seem quite commonsensical if we don’t read too much into them. They are:

1. Major research programs are built on exemplary texts that record exemplary experiments and interpretative accomplishments. Thus Newton’s *Principia* and Darwin’s *Origin* are what Kuhn now calls *exemplars*. These two books showed, by example, how to do science in a certain style, specifically how to interpret and apply major new theories. One of the terms derived from Greek for an exemplar of this sort is ‘paradigm’. Part of what Kuhn meant to capture by his use of that term is this: *science is built on exemplars*. Kuhn correctly notes that there are exemplars of very many different types, some at a very high level and others at a low level; Newton’s and Darwin’s books are high-level exemplars (i.e., paradigms). Low-level ones are ubiquitous in the teaching of science – for instance, the exemplary problems with which we force our students to cope in a freshman lab or the problems and problem solutions in a standard textbook. Such exemplars are the means by which we teach our students to become scientists; they are the cornerstones in the system of apprenticeship that we employ to handle that delicate job.
2. The practices of the scientists working in a given discipline are typically built on a series of complicated implicit agreements and understandings. These are very diverse in nature: they cover the basic assumptions of the discipline; the proper interpretation and application of various mathematical formulae; the reasons for choosing one technique or experimental organism over another; judgments regarding the relative reliability of various techniques, laboratories and even people; judgments regarding the social as well as the intellectual structuring of the discipline, and so on. Sociological frameworks of this sort, which help to structure the work, content, and education in a given field, Kuhn now calls *disciplinary matrices* (Kuhn 1970a, p. 271, 1974, p. 468 ff.). His original terminology treated the whole range of implicit agreements involved in such socially forged networks as *paradigms* because, he thought, the agreements came about without explicit articulation from the use of exemplars – i.e., the standard texts, techniques, problems, and problem solutions from which one learned as a student of the discipline.

We are now in a position to ask to what extent there is an evolutionary paradigm. Using Kuhn’s own separation of paradigms into exemplars and disciplinary matrices, this

question is transformed into two questions: is the practice of evolutionary biology correctly described as based on some central exemplars? The answer to this question is obviously affirmative. One need only mention Dobzhansky, Mayr, Simpson and Stebbins – or, in a different vein, sickle cell anemia, variation among hemoglobins, and *Biston betularia* – to see how easy it would be to establish this claim. The second question is whether some one disciplinary matrix dominates the practices of evolutionary biologists. This second question is a large one that cannot be properly resolved on this occasion. I shall, however, offer some good reasons for being skeptical about the presence of anything like a single disciplinary matrix during most of the history of modern evolutionary biology. Not least of these is the fact that evolutionary biology is not a single discipline, but a complex interdisciplinary field which lies in a region that overlaps onto the territory of very diverse disciplines.

Some Historical Notes

In the present section I offer a rough and ready treatment of some historical points that show how implausible it is to treat evolutionary biology before the development of the synthetic theory as falling within a single disciplinary matrix. In the next section I support the parallel conclusion with respect to the synthetic theory itself.

The large-scale historical point can be put rather simply. Darwin's *On the Origin of Species* (Darwin 1859) is, without question, an exemplar – it served as a paradigm in the first of the two senses distinguished above. It is a text to which evolutionary biologists have paid an enormous amount of attention ever since it was published and, to this day, even those evolutionary biologists who have not seriously read the *Origin* are deeply influenced by it. It is a work that has penetrated evolutionary theory and the practice of evolutionary biology very deeply. Yet in spite of this, it is arguable whether the *Origin* or any other influence has established a dominant disciplinary matrix within evolutionary biology.²

Among the many ways of getting at this issue by means of historical investigations I can pursue only one here, and that very sketchily. This is to examine the relationships among various versions of Darwinism. (It would also be useful to examine the many alternative theories that have played a major role in evolutionary biology at various times and places, but I haven't space to address this topic today.) In this connection, it is worth recalling that for a substantial portion of the history of evolutionary biology *no* version of Darwin's theory of evolution *by means of natural selection* was the dominant accepted theory. Indeed, in all of the relevant national

² Ernst Mayr (pers. commun.) suggests that the *Origin* established a definite theoretical framework or set of principles. He suggests that, after Darwin, descent with modification acquired a central place in biological reasoning that it had not had before, and that therefore it is a mistake to claim that Darwin failed to establish a dominant disciplinary matrix in evolutionary biology. This criticism is mistaken, for it fails to recognize that a disciplinary matrix (at least as Kuhn intends the term) is built on common problems, techniques, training, and standards of evaluation established by education *within a reasonably well-defined discipline*. Anatomists, biogeographers, zoologists, botanists, breeders, natural historians, etc., even if they are evolutionists sharing the *Origin* as an exemplar, do not share a disciplinary matrix. The best reading of the evidence, I believe, does not reveal a common disciplinary matrix for Darwinian evolutionists 1859-1909, even when one restricts one's attention to England.

traditions Darwinian theory received quite different interpretations so that, looked at from an international perspective, the Darwinian party did not share common assumptions of the sort Kuhn includes in disciplinary matrices. The central point is that it is implausible to claim that there was anything resembling a single disciplinary matrix in evolutionary biology at least until the general acceptance of the synthetic theory of evolution around the latter 1940s – and, as I will argue below, it is not really very plausible then.

In support of these claims, it is useful to begin with Mayr's point that Darwin put forward a congeries of theories (Mayr 1985). For present purposes I will mention only three: namely that evolution is gradual, that it consists in a process of descent with modification, and that the most significant evolutionary force among the many Darwin recognized is natural selection. I shall focus on the latter two to some extent in this section. Let us now recall the reception of Darwin's theories in very general terms. The initial success of the *Origin* did not (as is sometimes naively assumed) yield widespread acceptance of the theory of evolution *by means of natural selection*; at most it established that descent with modification could account for the major phenomena of biogeography, paleontology, and systematics, and for the adaptations of plants and animals. To be sure, the theory of natural selection played a major role in this initial success, for it offered a plausible mechanism by means of which evolutionary change could be seen as creating adaptations.³ Nonetheless, for a very long time the particular mechanisms of evolution were treated extremely pluralistically by most theorists – including Darwin himself, especially in the later editions of the *Origin* and in the *Descent of Man* – and there was an immense amount of debate over the claim that the historical path of evolutionary change was dominantly the effect of natural selection as opposed to saltatory mutation, inherited effects of use and disuse of organs, direct effect of climate, internal orthogenetic drives, and so on.

A central tenet of contemporary Darwinism is that natural selection is the predominant cause of evolutionary pattern. This claim was nowhere fully accepted in Darwin's day; Darwin himself lamented the failure of his work to convince his peers on this score. Indeed, as is shown by an examination of primary sources (Kellogg 1907, Seward 1909) and as is widely recognized in recent historical writings (Bowler 1983, Mayr 1982), belief in the importance of natural selection as a factor in evolution reached a nadir around 1909, the centenary of Darwin's birth and the fiftieth anniversary of the

³ Mayr (pers. commun.) considers this a myth, pointing out correctly that common descent was broadly accepted in spite of the fact that natural selection was rejected by most naturalists, including even T. H. Huxley. I think, nonetheless, that natural selection "broke the ice" for descent with modification. It made it seem plausible that a thoroughly naturalistic account could be given of adaptations, even to those who rejected Darwin's account of the role of natural selection in evolution. As (Lewontin 1983) points out (an article which Mayr reminded me of!), natural selection broke with the spirit of all prior evolutionary theories (such as Lamarck's). Those theories were "transformational," i.e., they required that the evolution within a lineage be a sum of the changes that occurred to individual organisms. Typically, such theories have difficulty with adaptation, requiring ad hoc or secondary causes to explain adaptations. Darwin's "variational" theory, in contrast, took variation as somehow given, so that the source of evolutionary change was some sort of external action upon available variation rather than a building up of new permanent variation within the organism for exploitation. (Darwin himself, to be sure, was obstinately pluralist; use and disuse of organs as a source of evolutionary change is a transformational mechanism, quite different, in this respect, than natural selection.)

publication of the *Origin*. Although it was nearly universally granted that Darwin's mechanism played *some* role in evolution, by this time there were relatively few defenders of the idea that natural selection is a major contributor – let alone *the* major contributor – to the fundamental patterns of evolutionary history.

Less well known except among specialist historians is the fact that each of the major national traditions interpreted Darwin quite differently (Glick 1974, Kohn 1985). I will speak, absurdly briefly, of England, France, Germany, and Russia in order to drive this point home. Although I am talking in very crude general terms, the sketch offered here is, I believe, an adequate first approximation. In England, descent with modification was rapidly accepted and natural selection taken seriously; the Darwinian theory came to be allied with gradualism and biometry. By the turn of the century, most Darwinians treated small and copious variations as the raw material for natural selection, emphasized the fine-grained character of adaptation, and stressed the causal importance of the intense Malthusian scrutiny of every variant as the key to evolutionary dynamics. In France, Darwin was treated as a utilitarian cheapener of Lamarck, offering nothing particularly new or interesting outside of the already available evolutionary theories. Even descent with modification had great difficulty in making its way and, insofar as it did, transformational and variational versions of the theory were not properly distinguished (see note 3). A few of Darwin's defenders emphasized his pluralism with regard to the mechanisms underlying evolution, but they conceded that he overstressed natural selection. In Germany, too, the distinction between Lamarckism and Darwinism was not very clear, but between the influence first of Haeckel and then of Weismann, Darwin's theory became associated with preformationism on two grounds: that the organism contained the history of its lineage (cf. the biogenetic law) and that the developmental unfolding of the organism was a consequence of the inherited materials produced in that history and a necessary condition for the independence of variation from environmental influence.⁴

In Russia, finally, Darwinism was reinterpreted to remove its Malthusian moment. Todes (Todes 1987, 1988) reviews this history, arguing that at least two major considerations influenced this stance. One of these is biological – the vast emptiness of the steppes, which were the central arena for the studies of Russian ecologists and naturalists. To the students of the ecology and evolution of the biota of this vast region, struggle against the climate seemed far more intense and important than intraspecific competition. The other influence was, in a sense, political (though common to the political left and the political right), and had to do with the widely acknowledged need to increase population in Russia in order to exploit available resources efficiently. Malthus, it seemed, was just wrong about Russia: increasing the population under the appropriate social arrangements was the means to guarantee *enough* food for everyone. As things stood, the primary factor holding down the population was the lack of sufficiently intense agriculture to produce food. But without sufficient population, it was impossible to institute appropriate agricultural and productive techniques, systems, and reforms.

Both of these influences made the Malthusian starting point utterly implausible to Russian theorists and led them to reinterpret Darwin's theory along lines ultimately

⁴ Mayr (pers. commun.) correctly cautions that Weismann and other panselectionists were very isolated by the turn of the century in Germany. Various forms of orthogenesis and mutationism were preferred by the majority of German biologists with evolutionary interests at that time.

popularized in the West by Kropotkin – i.e., to admit competition with the environment and between species, but to insist on the fundamental importance of *cooperation within species*. Such an approach was thoroughly integrated into the strong evolutionary tradition of Russian biology.

Although I have been speaking about the differences among national traditions, much the same sort of disagreement about the proper content of Darwinism occurred *within* many of these traditions. The differences between transformational and variational theories of evolutionary mechanisms (see note 3) were by no means clear; toward the turn of the century almost everyone except Weismann, whose speculations were widely rejected, was confused in this respect. Again, there were serious disagreements regarding just what should be accepted from Darwin and what should count as the core of Darwinian theory. Worse yet, insofar as Darwin's various subtheories were recognized, the interrelations between them became uncertain. Was gradualism required to make sense of natural selection, or to support descent with modification? Such questions had become extraordinarily troublesome. Many figures wished to claim the authority of Darwin in support of their own views, while also rejecting, in specific contexts, for specific purposes, various important Darwinian doctrines. The resultant tangles became extremely complicated.⁵

The lay of the land as I am depicting it can be nicely summarized by suggesting that the history of the first 75 or 100 years of Darwinism could be written under the rubric of *Struggling for the Mantle of Darwin*. Throughout this history, the *Origin* and some of Darwin's other writings served as exemplars, but there were constant attempts to reinterpret Darwin's ambiguous and pluralistic theory along widely divergent lines. Thus, the *Origin* was read very differently by different parties, and it was used to support a great many mutually incompatible positions. Frequently these divergent readings were intended to help forge the sort of consensus that Kuhn has characterized as the crucial, though tacit, center of a disciplinary matrix and to convert the resultant consensus into the doctrinal core of evolutionary biology. The fact that many divergent biological disciplines, often drawing on different problems and techniques, were affected by these divergences, made the task of reaching full consensus very difficult.

Why should *this* exemplary text have served as such a symbol of authority? Because very many evolutionists – with the exception of the French and certain of the more extreme Lamarckian and orthogenetic opponents of Darwin – wished to draw on Darwin's reputation as founder of mainstream evolutionary theory and as the most influential naturalist/evolutionist of the age. But the struggle to cloak such extremely divergent doctrines in the mantle of Darwin, which continues even to this day, is a nice symptom of the fact that there was not and is not a single disciplinary matrix in evolutionary biology. I conclude that the influence of Darwinism on neighboring sciences should not be understood in terms of the influence of 'the' evolutionary paradigm.

The Evolutionary Synthesis

The synthetic theory of evolution is a moving target. Nonetheless, in first approximation, it can be characterized fairly briefly, for it was put forward by a series of founding

⁵ [Added in 2003:] For an extreme account of the trouble that results from these considerations, see (Hull 1985), which denies that there is no set of shared doctrines adequate to characterize the common features of the different versions of Darwinism.

documents in the period from 1937 to, roughly, 1950. I take the first of these to be (Dobzhansky 1937) and the last (Stebbins 1950). Among the more important books along the way one must include those by Mayr (Mayr 1942) and (Simpson 1944), though many other writings should be cited as well.

The central point of the synthesis was to demonstrate the adequacy of Mendelian genetics (including especially population genetics) plus an updated version of Darwin's theory of evolution by means of natural selection, joined in the manner illustrated in the founding documents, to serve as the theoretical basis for explaining all evolutionary phenomena. The following doctrines are characteristic of the synthetic theory: the immense variability of natural populations, the genetic (indeed, Mendelian) basis for evolution, the importance of geographic speciation, the adaptive nature of observed differences among organisms, the primacy of natural selection in causing the evolutionary patterns found in the paleontological record, the gradualness of evolution, the compatibility of all macroevolutionary phenomena with the mechanisms of (gradual) microevolution (thus ruling out saltational models), and the importance of what Mayr called 'population thinking'.⁶ Bruce Wallace's paper in this volume (Wallace 1989) exemplifies quite well the sort of stance which I would include within the synthesis.

In certain respects the synthetic theory, so-called, is better viewed as a treaty than as a theory.⁷ By this I mean that one could not use the population genetic foundations of the theory to predict or retrodict large-scale evolutionary patterns or fundamental features of the taxonomic system. Nor can population genetics alone determine the prevalence, evolutionary importance, or historical trajectory of major traits like sexuality – indeed it cannot even provide a full answer to Darwin's problem, the origin of species. Yet, in spite of this, the synthetic theory did a great deal to reduce the conflict between evolutionists belonging to different disciplines. For example, it served to contravene the paleontologists' belief that Mendelian variation cannot offer a sufficient explanation for macroevolutionary phenomena, to undermine the geneticists' early insistence that genetic (and hence evolutionary) change is discontinuous and saltational, and to counteract the systematists' conviction that laboratory experiments on mutations and Mendelian variation were irrelevant to the sorts of variation and evolutionary change found in natural populations. Precisely because the synthetic theory aimed 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. It allowed the claims about the *patterns* and *results* of evolution to be drawn from other disciplines while insisting that the *mechanisms* revealed by population genetics were the only ones needed to bring those patterns about.

⁶ This list deemphasizes the contribution of genetics to the evolutionary synthesis. It is based on Mayr's gloss (Mayr 1980) on various contributions to the synthetic theory. Mayr (pers. commun.) considers the two most important contributions of genetics to the synthesis to be evidence for the facts that "inheritance is particulate, not blending; and that inheritance is hard, not soft (Lamarckian)." He adds that these contributions "have comparatively little to do with population genetics."

⁷ The term 'treaty' is taken from (Depew and Weber 1988). Both that essay and (Burian 1988) amplify on some of the points made here. See below for some connections with other analyses of the synthetic theory as a metatheory or a schematic theory.

Not surprisingly, the evolutionary synthesis has changed with time. For one thing, the tools available to theorists and field workers have grown considerably more sophisticated, especially with the introduction of computers and of molecular techniques. One controversial claim of interest to us about the developments from, say, 1950 to 1970, a claim which I believe is correct, is that the synthesis hardened, at least to some extent, into unexamined dogma, sometimes dismissing viable alternatives on the basis of prejudice rather than hard evidence (Gould 1983). Early on, the very weakness of the compatibility claim was viewed as one of the *strengths* of the synthesis. In principle, virtually all the known phenomena and patterns that ought to be explained by an evolutionary theory *could* be explained by some variant of 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.

There is no room here to go into examples in detail, but I shall cite three of the many that could be adequately documented to illustrate the point. These are the treatment by many theorists of the late Sewall Wright’s shifting balance theory (which, after the mid-fifties was frequently dismissed as placing far too great an emphasis on fixation of random variants in small populations), the change in Simpson’s views about quantum evolution and its relationship to natural selection, and the increasing panselectionism of many of the leading figures in the field. (Another symptom of this change, pointed out to me some years ago by Marjorie Grene, is the disappearance from later editions of the founding texts – and from the literature of the theorists of the synthesis generally – of people like Goldschmidt, Robson and Richards, Schindewolf, and Willis. These figures had served as rhetorical targets in the founding debates, and their disappearance signals the fact that their non-selectionist alternatives came to be considered irrelevant and no longer threatening.)

If this characterization of the synthesis as a treaty is approximately correct, it enforces the conclusion that I wish to draw: that there is no single disciplinary matrix to which the adherents of the synthesis subscribe. Nor should this be surprising: the scientific advocates of the synthesis are drawn from systematics, population genetics, paleontology, botany, zoology, biogeography, and an immense variety of additional disciplines. To that extent, even though their commitments overlap and even though they share some exemplary texts, their disciplinary allegiances (and their primary training) belong to very different fields. It should not take much reflection on the consequences of this fact to recognize that their socialization as scientists prevents them from sharing a common disciplinary matrix, the supposed disciplinary matrix of evolutionary biology or evolutionary theory. In the last section of the paper I will explore a few consequences of this fact for the future of that theory. But first I shall address one more topic.

The Synthetic Theory as a Theory of History

The synthetic theory, like Darwinism generally, claims that the details and many of the basic patterns of organismic evolution are, at heart, historically contingent. Gould has argued persuasively that Darwin’s central accomplishment in this regard was to construct a theory that treated adaptation as response to the historical sequence of selective demands of the environment (including other organisms), a theory that accounted for taxonomic and morphological order in terms of “historical pathway, pure and simple”

(Gould 1986, p. 60). These Darwinian explanations contrast with alternatives couched in terms of “intrinsic purpose and meaning,” or of laws of form, and so on. For Darwinians, Gould claims, homology requires, and is explained by, common descent, whereas similarity of functional form without common descent (analogy), however striking, is accounted for by the adaptive power of selection. Many readers will recognize that this is a very substantial and controversial claim, for it commits one to the view that the only correct account of the identity of homologous structures – e.g., of a particular metatarsal in different vertebrates – is identity by descent.

We recognize the occurrence of biological evolution and delineate phylogenies in part by means of “accidents of history.” The term is apt. Cladistic classifications, as I understand them, place organisms into taxa defined in terms of shared derived characters (“synapomorphies” in cladistic terminology). While our assessments of particular traits as synapomorphies may be mistaken, the principle behind such classifications is fundamentally sound. And the corresponding practice seems to me to generate an interesting argument against the derivation of basic evolutionary patterns from the fundamental laws or axioms of evolutionary theory.

Compare, for example, biological with stellar evolution. Stellar evolution is transformational – i.e., in the absence of highly unusual interactions with other cosmic bodies, the stages of the life history of each star can be derived from its intrinsic properties (mass and composition) and appropriate initial or boundary conditions (Lewontin 1983, p. 63). In the terminology of some philosophers of biology (Brandon 1982b, 1990, chap. 3), the effects of such other factors as the *history* of the materials out of which a star was formed (which almost certainly came from other stars) are ‘screened off’ by the physical properties of the star. That is, “accidental” properties like those relevant to evolutionary studies of biological entities are not needed and are of no help in determining either the parentage or the 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 rather than interactions with their environment or with one another. In part it is because (in the absence of strong interactions with other stars) the evolution of the ensemble of stars is, in effect, a straightforward summation of the evolution of each individual star.

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, though the phenomenon they illustrate is ubiquitous. In the end, both cladistics and evolutionary biology as a whole depend deeply on the contingent fact of evolutionary tinkering (Jacob 1977).

Since evolutionary theory is concerned, among other things, with analyzing genealogical connections and patterns of genealogical affinity among organisms, it must build upon the essential historicity of biological evolution. The same historicity applies when the aim is to describe patterns of evolution among DNAs, proteins, organisms, taxa, or clades, or to develop evolutionary laws relating, for example, morphological change to cladogenesis or phylogeny.

This historicity is unavoidable; it cannot be escaped by developing 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, statistically⁸). 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*. I have in mind H. E. H. Paterson’s account of Specific Mate Recognition Systems, and the role it has played in the thinking of people like Elisabeth Vrba and Niles Eldredge.⁹ To the extent that separate lineages acquire independent evolutionary fates because the organisms of those lineages employ contingent and accidental differences as cues in mate recognition, the entry of historical accidents into a sound account of evolutionary history is forced on us by the organisms themselves.

This historical component of the Darwinian explanation of underlying form has often been overlooked. Like other historical theories, evolutionary theory must presuppose ahistorical laws as background. These in turn (assuming they are correct) provide some of the constraints¹⁰ within which history runs its course. Nonetheless the theory must also offer a means for weighing the causal relevance and relative importance of multiple processes, patterns, and singularities whose historical roles are not wholly determined by the background laws. For this reason, as well as others (e.g., the complications added by the hierarchical structuring of organisms and of evolutionary

⁸ I have in mind results of the sort that Stuart Kauffman has obtained in simulating some of the general properties of gene regulation networks. Relatively accessible presentations of some of his results are available in (Kauffman 1985, 1986). (Kauffman 1993) brings these lines of work up to date. This extraordinarily promising book covers an enormous range of topics – origin of life, coevolution of organisms and environments, evolution of complex systems and their adaptations, evolution of ligand binding and catalytic function in proteins, evolution of a connected metabolism, evolution of patterns of gene regulation, evolution of development and its regulation, and so on. [Added in 2003:] for a more popular presentation of the results of this book, see also (Kauffman 1995).

⁹ Cf., e.g., (Paterson 1982). This line of work is discussed by (Eldredge 1985); further references to related work by Eldredge, Vrba, and others may be found there.

¹⁰ The theme of ahistorical universals is nicely developed by Kauffman. In light of his work, it is useful to distinguish between universals resting on fundamental physico-chemical laws and those resting on statistically near-universal features of the relevant classes of complex systems (such as those mentioned above, n. 8). The theme of constraints is usefully discussed in (Maynard Smith, et al. 1985). In their terminology, constraints deriving from physico-chemical laws would be classed as ‘universal’, those from the general features of complex systems as (relatively) ‘local’.

processes¹¹), evolutionary theory is, and will continue to be, characterized by a proliferation of alternative models and smaller scale theories applicable to particular cases. To this extent the fundamental laws and principles of the theory 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 basic evolutionary principles, even when supplemented with appropriate boundary or initial conditions, do not provide the wherewithal for a full derivation of major evolutionary patterns or the resolution of typical evolutionary disputes.¹² This is one 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 importance of ecological catastrophes, and the debates over the units of selection and the relevance of hierarchical structure). In all these cases we are dealing with questions of relative frequency. In all these cases, examples can be found that support the existence of whichever pattern or the efficacy of whichever mechanism. And, in all these cases, the patterns and mechanisms are compatible with the leading principles of the synthetic theory *provided that those principles are stated abstractly enough*.¹³

Pluralism

The distance from the abstract principles of variation, heritability, and differential fitness and the concepts on which they are founded to an account of the types and frequencies of the patterns of evolution and their causes is very great indeed. Their very abstractness means that the principles are not sufficient, by themselves, to resolve the disputes like those just mentioned: the real work must go on closer to the data and with specific models. And many of the models and scenarios in current use involve *specifications* of the abstract 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 no suitable radical alternative to the synthetic theory is in sight, *the fate of the synthesis as a coherent system of particular beliefs about evolutionary causes and patterns is still up in the air*.

¹¹ Hierarchical structure and its importance are discussed in passing in (Burian 1988). A good start on the literature may be gotten from (Eldredge 1985) and the following allied sources: (Eldredge and Salthe 1984, Grene 1987, Salthe 1985, Vrba and Eldredge 1984). These issues also connect in interesting ways with the huge literature on the units of selection problem.

¹² Cf. (Brandon 1978, 1982b). Brandon argues that evolutionary theory gets its empirical content from the *specification* of these principles so that they pertain to particular cases (e.g., particular organisms and environments). The principles provide the schemata which, when specified, make empirical claims. It is for this reason that I count evolutionary theory as a schematic theory. Related positions, using various labels, have been taken by Caplan, Tuomi, Wasserman, and others; some references are supplied in (Burian 1988).

¹³ The *locus classicus* for such statements is (Lewontin 1970). Lewontin's abstract version of the theory of natural selection can be boiled down to the following formula: heritable variation of fitness yields evolution by means of natural selection. This formula is compatible with group selection, non-Mendelian systems of inheritance, and even inheritance of acquired characters. To that extent, the formula seeks to represent the core of Darwinism, not the synthetic theory.

This characterization may appear unduly pessimistic to some. I wish to counteract this appearance. On the one hand, the situation does not call for pessimism – new techniques now enable us to learn an immense amount that, until recently, was far beyond our means. On the other hand, the pessimism about the limited power of fundamental theories is, I believe, justified. Evolutionary biology is, unavoidably, an historical discipline, with a rich, but still highly limited base of data available to it. Given this, it is unreasonable to expect to derive its principal results from a theory whose core consists solely of abstract or ahistorical (time symmetrical) laws. To put the point in a rather extreme way: I suspect that even such biologically basic matters as the specific content of the genetic code and the unique role of DNA in cellular organisms are contingent outcomes of historical processes. Given current knowledge, it seems unlikely that these fundamental properties of terrestrial organisms are 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. Should this be correct, there can be little question but that the course of evolution, even on a fairly large scale, is fraught with the consequences of historical accidents and contingencies.

The point is not that ahistorical universals are irrelevant or unimportant – quite the contrary, for they, plus the relevant boundary conditions (such as those pertaining to the primordial earth), set the baseline for what would occur in the absence of selection or of any processes peculiar to living systems. Physical and chemical laws are causally prior to the origin of life. Other universals may pertain specifically to entities exhibiting certain of the structural complexities characteristic of living things. But no matter: *all* relevant universals provide the setting within which the contingent history of living beings is played out. Just as the study of the geology of our planet cannot be properly pursued without reliance on both the fundamental laws of physics and chemistry as applied to planets and the specific accidental conditions pertaining to this planet, so the study of evolution generally and of the evolution of living forms on this planet cannot be properly pursued without reliance on the underlying laws of physics and chemistry plus any genuine laws pertaining to the features of complex systems of the sorts that happen to have evolved here. But this leaves an important question open: *how much of the shape of the evolutionary history that we study has been determined by the accidents of circumstance (from molecular abundances at particular times and places to continental drift, volcanoes, and cometary impacts) that have impinged on the biota of the planet?* Such problems are found at all levels, from the molecular to the macroevolutionary.

To solve such problems, one needs to determine the “inertial baseline” from which biotic evolution and/or selection depart – e.g., to determine what would happen to relevant sorts of complex genetic and biochemical systems, once they were up and running, in the absence of selection. A promising line of inquiry bearing on this topic has recently been opened up by Stuart Kauffman (cf. esp. Kauffman 1993). He shows how one can evaluate deep statistical features of very general classes of genetic systems so as to reveal important ensemble properties that would be manifested by genomes, proteins, cells, and organisms *in the absence of selection*. If this can be done, whether with Kauffman’s protocols or with others currently being developed, it may be possible to make realistic estimates of the contribution of selection to the present genomic structures

of organisms and of the extent to which similar structures should have been expected in the absence of selection.

More generally, various lines of work promise to yield improved estimates of the specific contributions of selection, drift, the structure of the environment, and rare catastrophes, as well as a better understanding of the patterns and structures that would arise no matter what as the automatic consequences of DNA and chromosomal mechanics and other structure-producing features of organisms. As a result, we can expect new data and new theoretical footholds that can be put to use in evaluating the preponderance and importance of alternative modes and patterns of evolution and the various causes of those patterns. It is too early to tell whether this will enable us to resolve some of the longstanding issues that have plagued evolutionary theorists, but there are plenty of avenues to explore.

The apparent importance of the accidents of history, revealed by the fossil record and the distribution of properties among organisms, suggests that those accidents have played an enormous role in shaping the biota we study and the evolutionary patterns that we seek to understand. It is of great interest to learn to what extent this is true. Indeed, one of the most challenging intellectual problems posed by evolutionary biology is developing the proper tools to analyze the interplay between accident and law in shaping the familiar world around us.

Morals for Theorists at the Crossroads

It would be an act of hubris to try to predict the future of evolutionary biology in detail, but especially so for an interested bystander like me. Furthermore, a serious estimate of where evolutionary theory is headed should examine a number of themes not here addressed. One of these concerns the role of hierarchies of various sorts in shaping evolutionary history. A second concerns the role of molecular work in transforming the practice of evolutionary biology. A third concerns the proper analysis of the logical structure of evolutionary theory and the ways in which it acquires its empirical content.¹⁴ The views expressed below would be considerably enriched by developing these themes at length, but space prohibits opening up any additional topics. In any case, the two issues that dominate this paper – the thoroughly interdisciplinary character of evolutionary biology and the historicity of the phenomena it studies – yield some ideas about the way things are likely to go. I will close by putting a few of these forward in the hope of provoking lively and thoughtful responses.

The historicity of evolutionary phenomena suggests certain limits on what can be expected from evolutionary theory. For this purpose, I include with evolutionary theory recent attempts to extend that theory or to connect it with other grand theories, like the attempts of Brooks and Wiley or Wicken, for example, to connect the theory of evolution to non equilibrium thermodynamics (NET) (Brooks and Wiley 1986; cf. also Dyke 1987, Weber, Depew and Smith 1988, Wicken 1987). NET is, of course, relevant to evolution, and it may tell us a fair amount about the character of the stable and self-perpetuating systems that are possible in a wide range of circumstances. But such considerations can

¹⁴ I find Brandon's argument, characterized in n. 12, persuasive; the principle of natural selection, characterized below, obtains its empirical content from the specifications of degrees of adaptedness for particular kinds of biological entities and kinds of environments.

capture at the very most certain baselines and thermodynamic constraints within which evolution occurs.

Richard Lewontin has suggested that the history of life can well be viewed as a history of the ways organisms have found to get around constraints (Maynard Smith, et al. 1985, p. 282). Unless theories that characterize some constraints on organismic evolution (as NET does by studying ‘universal’ constraints on the evolution of various kinds of dissipative structures) can also capture the role of particular historical circumstances in the breaking of constraints – and also, I would add, in determining lineage splitting, particular features of organisms or species, and the evolutionary effects of biological interactions and behaviors – those theories will not be able to capture the interaction between law and history that characterizes evolution.¹⁵

It is this interaction between law and history that requires any satisfactory general theory of evolution to have the peculiar character of a *schematic theory*.¹⁶ By this I mean that while such a theory provides a framework for describing and explaining evolutionary sequences and patterns, it is necessary to fill in that framework by means of particular empirical analyses of the historical features and circumstances of the organisms in question, including the peculiarities of their environment and the characteristics of traits and behaviors that will be advantageous in that environment. Thus, there is no character that is, of its own right, of high adaptive value; the adaptive values of all characters are relative to (partly accidental) historical circumstances.

It is here that the logical structure of the synthetic theory is so crucial. Robert Brandon’s analysis of that structure, which is consilient with the position I am now advocating, makes the point nicely. Brandon states the principle of natural selection as follows:

(Probably) If a is better adapted than b in E , then a will have more offspring than b in E (Brandon 1982a, p. 432).

The interesting thing about this interpretation of the principle of natural selection is that, thus formulated, it provides no guidance regarding which traits or behaviors in which environments yield better adaptation than alternative traits. It is at just this point that empirical content is supplied to the principle by work undertaken in various independent disciplines, and it is at just this point that the relevance of the sorts of historical knowledge on which I have been focusing becomes inescapable.

If, indeed, historical and empirical work imported from a great variety of disciplines is required at this point, the character of the synthetic theory as a treaty is closely connected to its logically schematic structure. And this structure, in turn, is tightly connected to the following four home truths: First, there are very many ways that organisms can earn livings. Second, an organism’s success in earning a living depends not only on luck, but also on its environment; including who its competitors are. Third, no adequate answer as to how it is possible to earn a living can be derived primarily from general thermodynamic or evolutionary considerations, important as these are. And fourth, there are ways of achieving reproductive success without being particularly good at making a living. If we take these home truths seriously, it should be clear that no single disciplinary matrix can provide satisfactory guidance regarding the issues raised within

¹⁵ Kauffman’s work, insofar as I understand it, has some chance of meeting these desiderata.

¹⁶ See the references and discussion in n. 12.

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basic evolutionary theory. The lack of a single dominant disciplinary matrix in evolutionary biology is a consequence of the nature of evolutionary phenomena, and particularly of the role of historical accidents in affecting the evolutionary success, failure, and transformation of lineages. For this reason, I submit, we would be foolish to expect the unification of evolutionary theory within a single paradigm – and, what's more, we should count the failure to achieve such unification as a Good Thing.

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