Is a New and General Theory of Evolution Emerging?

Stephen Jay Gould

Paleobiology, Vol. 6, No. 1 (Winter, 1980), 119-130.

Paleobiology, 6(1), 1980, pp. 119–130

Is a new and general theory of evolution emerging?

Stephen Jay Gould

Abstract.—The modern synthesis, as an exclusive proposition, has broken down on both of its fundamental claims: extrapolationism (gradual allelic substitution as a model for all evolutionary change) and nearly exclusive reliance on selection leading to adaptation. Evolution is a hierarchical process with complementary, but different, modes of change at its three major levels: variation within populations, speciation, and patterns of macroevolution. Speciation is not always an extension of gradual, adaptive allelic substitution to greater effect, but may represent, as Goldschmidt argued, a different style of genetic change—rapid reorganization of the genome, perhaps non-adaptive. Macroevolutionary trends do not arise from the gradual, adaptive transformation of populations, but usually from a higher-order selection operating upon groups of species, while the individual species themselves generally do not change following their geologically instantaneous origin. I refer to these two discontinuities in the evolutionary hierarchy as the Goldschmidt break (between change in populations and speciation) and the Wright break (between speciation and trends as differential success among species).

A new and general evolutionary theory will embody this notion of hierarchy and stress a variety of themes either ignored or explicitly rejected by the modern synthesis: punctuational change at all levels, important non-adaptive change at all levels, control of evolution not only by selection, but equally by constraints of history, development and architecture—thus restoring to evolutionary theory a concept of organism.

Stephen Jay Gould. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138

Accepted: October 15, 1979

I. The Modern Synthesis

In one of the last skeptical books written before the Darwinian tide of the modern synthesis asserted its hegemony, Robson and Richards characterized the expanding orthodoxy that they deplored:

> The theory of Natural Selection . . . postulates that the evolutionary process is unitary, and that not only are groups formed by the multiplication of single variants having survival value, but also that such divergences are amplified to produce adaptations (both specializations and organization). It has been customary to admit that certain ancillary processes are operative (isolation, correlation), but the importance of these, as active principles, is subordinate to selection (1936, pp. 370–371).

Darwinism, as a set of ideas, is sufficiently broad and variously defined to include a multitude of truths and sins. Darwin himself disavowed many interpretations made in his name (1880, for example). The version known as the "modern synthesis" or "Neo-Darwinism" (different from what the late 19th century called Neo-Darwinism—see Romanes, 1900) is, I think, fairly characterized in its essentials by Robson and Richards. Its foundation rests upon two major premises: (1) Point mutations (micromutations) are the ultimate source of variability. Evolutionary change is a process of gradual allelic substitution within a population. Events at broader scale, from the origin of new species to long-ranging evolutionary trends, represent the same process, extended in time and effect—large numbers of allelic substitutions incorporated sequentially over long periods of time. In short, gradualism, continuity and evolutionary change by the transformation of populations. (2) Genetic variation is raw material only. Natural selection directs evolutionary change. Rates and directions of change are controlled by selection with little constraint exerted by raw

0094–8373/80/0601–0011/$1.00

material (slow rates are due to weak selection, not insufficient variation). All genetic change is adaptive (though some phenotypic effects, due to pleiotropy, etc., may not be). In short, selection leading to adaptation.

All these statements, as Robson and Richards also note, are subject to recognized exceptions—and this imposes a great frustration upon anyone who would characterize the modern synthesis in order to criticize it. All the synthesists recognized exceptions and "ancillary processes," but they attempted both to prescribe a low relative frequency for them and to limit their application to domains of little evolutionary importance. Thus, genetic drift certainly occurs—but only in populations so small and so near the brink that their rapid extinction will almost certainly ensue. And phenotypes include many non-adaptive features by allometry and pleiotropy, but all are epiphenomena of primarily adaptive genetic changes and none can have any marked effect upon the organism (for, if inadaptive, they will lead to negative selection and elimination and, if adaptive, will enter the model in their own right). Thus, a synthesist could always deny a charge of rigidity by invoking these official exceptions, even though their circumscription, both in frequency and effect, actually guaranteed the hegemony of the two cardinal principles. This frustrating situation had been noted by critics of an earlier Darwinian orthodoxy, by Romanes writing of Wallace, for example (1900, p. 21):

> [For Wallace,] the law of utility is, to all intents and purposes, universal, with the result that natural selection is virtually the only cause of organic evolution. I say 'to all intents and purposes,' or 'virtually,' because Mr. Wallace does not expressly maintain the abstract impossibility of laws and causes other than those of utility and natural selection; indeed, at the end of his treatise, he quotes with approval Darwin's judgement, that 'natural selection has been the most important, but not the exclusive means of modification.' Nevertheless, as he nowhere recognizes any other law or cause of adaptive evolution, he practically concludes that, on inductive or empirical grounds, there *is* no such other law or cause to be entertained.

Lest anyone think that Robson and Richards, as doubters, had characterized the opposition unfairly, or that their two principles represent too simplistic or unsubtle a view of the synthetic theory, I cite the characterization of one of the architects of the theory himself (Mayr 1963, p. 586—the first statement of his chapter on species and transspecific evolution):

> The proponents of the synthetic theory maintain that all evolution is due to the accumulation of small genetic changes, guided by natural selection, and that transspecific evolution is nothing but an extrapolation and magnification of the events that take place within populations and species.

The early classics of the modern synthesis—particularly Dobzhansky's first edition (1937) and Simpson's first book (1944)—were quite expansive, generous and pluralistic. But the synthesis hardened throughout the late 40's and 50's, and later editions of the same classics (Dobzhansky 1951; Simpson 1953) are more rigid in their insistence upon micromutation, gradual transformation and adaptation guided by selection (see Gould 1980 for an analysis of changes between Simpson's two books). When Watson and Crick then determined the structure of DNA, and when the triplet code was cracked a few years later, everything seemed to fall even further into place. Chromosomes are long strings of triplets coding, in sequence, for the proteins that build organisms. Most point mutations are simple base substitutions. A physics and chemistry had been added, and it squared well with the prevailing orthodoxy.

I well remember how the synthetic theory beguiled me with its unifying power when I was a graduate student in the mid-1960's. Since then I have been watching it slowly unravel as a universal description of evolution. The molecular assault came first, followed quickly by renewed attention to unorthodox theories of speciation and by challenges at the level of macroevolution itself. I have been reluctant to admit it—since beguiling is often forever—but if Mayr's characterization of the synthetic theory is accurate, then that theory, as a general proposition, is effectively dead, despite its persistence as textbook orthodoxy.

II. Reduction and Hierarchy

The modern synthetic theory embodies a strong faith in reductionism. It advocates a smooth extrapolation across all levels and scales—from the base substitution to the origin of higher taxa. The most sophisticated of leading introductory textbooks in biology still proclaims:

> [Can] more extensive evolutionary change, macroevolution, be explained as an outcome of these microevolutionary shifts. Did birds really arise from reptiles by an accumulation of gene substitutions of the kind illustrated by the raspberry eye-color gene.
>
> The answer is that it is entirely plausible, and no one has come up with a better explanation . . . . The fossil record suggests that macroevolution is indeed gradual, paced at a rate that leads to the conclusion that it is based upon hundreds or thousands of gene substitutions no different in kind from the ones examined in our case histories (Wilson et al. 1973, pp. 793–794).

The general alternative to such reductionism is a concept of hierarchy—a world constructed not as a smooth and seamless continuum, permitting simple extrapolation from the lowest level to the highest, but as a series of ascending levels, each bound to the one below it in some ways and independent in others. Discontinuities and seams characterize the transitions; "emergent" features not implicit in the operation of processes at lower levels, may control events at higher levels. The basic processes—mutation, selection, etc.—may enter into explanations at all scales (and in that sense we may still hope for a general theory of evolution), but they work in different ways on the characteristic material of divers levels (see Bateson 1978 and Koestler 1978, for all its other inadequacies, for good discussions of hierarchy and its anti-reductionistic implications; Eldredge and Cracraft 1980).

The molecular level, which once seemed through its central dogma and triplet code to provide an excellent "atomic" basis for smooth extrapolation, now demands hierarchical interpretation itself. The triplet code is only machine language (I thank E. Yates for this appropriate metaphor). The program resides at a higher level of control and regulation—and we know virtually nothing about it. With its inserted sequences and jumping genes, the genome contains sets of scissors and pots of glue to snip and unite bits and pieces from various sources. Thirty to seventy percent of the mammalian genome consists of repetitive sequences, some repeated hundreds or thousands of times. What are they for (if anything)? What role do they play in the regulation of development? Molecular biologists are groping to understand this higher control upon primary products of the triplet code. In that understanding, we will probably obtain a basis for styles of evolutionary change radically different from the sequential allelic substitutions, each of minute effect, that the modern synthesis so strongly advocated. The uncovering of hierarchy on the molecular level will probably exclude smooth continuity across other levels. (We may find, for example, that structural gene substitutions control most small-scale, adaptive variation within local populations, while disruption of regulation lies behind most key innovations in macroevolution.)

The modern synthesis drew most of its direct conclusions from studies of local populations and their immediate adaptations. It then extrapolated the postulated mechanism of these adaptations—gradual, allelic substitution—to encompass all larger-scale events. The synthesis is now breaking down on both sides of this argument. Many evolutionists now doubt exclusive control by selection upon genetic change within local populations. Moreover, even if local populations alter as the synthesis maintains, we now doubt that the same style of change controls events at the two major higher levels: speciation and patterns of macroevolution.

III. A Note on Local Populations and Neutrality

At the level of populations, the synthesis has broken on the issue of amounts of genetic variation. Selection, though it eliminates variation in both its classical modes (directional and, especially, stabilizing) can also act to preserve variation through such phenomena as overdominance, frequency dependence, and response to small-scale fluctuation of spatial and temporal environments. Nonetheless, the copiousness of genetic variation, as revealed first in the electrophoretic techniques that resolve only some of it (Lewontin and Hubby 1966; Lewontin 1974), cannot be encompassed by our models of selective control (of course, the models, rather than nature, may be wrong). This fact has forced many evolutionists, once stout synthesists themselves, to embrace the idea that alleles often drift to high frequency or fixation, and that many common variants are therefore neutral or just slightly deleterious. This admission lends support to a previous interpretation of the approximately even ticking of the molecular clock (Wilson 1977)—that it reflects the neutral status of most changes in structural genes rather than a grand averaging of various types of selection over time.

None of this evidence, of course, negates the role of conventional selection and adaptation in molding parts of the phenotype with obvious importance for survival and reproduction. Still, it rather damps Mayr's enthusiastic claim for "all evolution . . . guided by natural selection." The question, as with so many issues in the complex sciences of natural history, becomes one of relative frequency. Are the Darwinian substitutions merely a surface skin on a sea of variation invisible to selection, or are the neutral substitutions merely a thin bottom layer underlying a Darwinian ocean above? Or where in between?

In short, the specter of stochasticity has intruded upon explanations of evolutionary *change*. This represents a fundamental challenge to Darwinism, which holds, as its very basis, that random factors enter only in the production of raw material, and that the deterministic process of selection produces change and direction (see Nei 1975).

IV. The Level of Speciation and the Goldschmidt Break

Ever since Darwin called his book *The Origin of Species,* evolutionists have regarded the formation of reproductively isolated units by speciation as a fundamental process of large-scale change. Yet speciation occurs at too high a level to be observed directly in nature or produced by experiment in most cases. Therefore, theories of speciation have been based on analogy, extrapolation and inference. Darwin himself focused on artificial selection and geographic variation. He regarded subspecies as incipient species and viewed their gradual, accumulating divergence as the primary mode of origin for new taxa. The modern synthesis continued this tradition of extrapolation from local populations and used the accepted model for adaptive geographic variation—gradual allelic substitution directed by natural selection—as a paradigm for the origin of species. Mayr's (1942, 1963) model of allopatric speciation did challenge Darwin's implied notion of sympatric continuity. It emphasized the crucial role of isolation from gene flow and did promote the importance of small founding populations and relatively rapid rates of change. Thus, the small peripheral isolate, rather than the large local population in persistent contact with other conspecifics, became the incipient species. Nonetheless, despite this welcome departure from the purest form of Darwinian gradualism, the allopatric theory held firmly to the two major principles that permit smooth extrapolation from the *Biston betularia* model of adaptive, allelic substitution: (i) The accumulating changes that lead to speciation are adaptive. Reproductive isolation is a consequence of sufficient accumulation. (ii) Although aided by founder effects and even (possibly) by drift, although dependent upon isolation from gene flow, although proceeding more rapidly than local differentiation within large populations, successful speciation is still a cumulative and sequential process powered by selection through large numbers of generations. It is, if you will, Darwinism a little faster.

I have no doubt that many species originate in this way; but it now appears that many, perhaps most, do not. The new models stand at variance with the synthetic proposition that speciation is an extension of microevolution within local populations. Some of the new models call upon genetic variation of a different kind, and they regard reproductive isolation as potentially primary and non-adaptive rather than secondary and adaptive. Insofar as these new models be valid in theory and numerically important in application, speciation is not a simple "conversion" to larger effect of processes occurring at the lower level of adaptive modelling within local populations. It represents a discontinuity in our hierarchy of explanations, as the much maligned Richard Goldschmidt argued explicitly in 1940.

There are many ways to synthesize the swirling set of apparently disparate challenges that have rocked the allopatric orthodoxy and established an alternative set of models for speciation. The following reconstruction is neither historically sequential nor the only logical pathway of linkage, but it does summarize the challenges—on population structure, place of origin, genetic style, rate, and relation to adaptation—in some reasonable order.

1. Under the allopatric orthodoxy, species are viewed as integrated units which, if not actually panmictic, are at least sufficiently homogenized by gene flow to be treated as entities. This belief in effective homogenization within central populations underlies the allopatric theory with its emphasis on *peripheral* isolation as a precondition for speciation. But many evolutionists now believe that gene flow is often too weak to overcome selection and other intrinsic processes within local demes (Ehrlich and Raven 1969). Thus, the model of a large, homogenized central population preventing local differentiation and requiring allopatric "flight" of isolated demes for speciation may not be generally valid. Perhaps most local demes have the required independence for potential speciation.

2. The primary terms of reference for theories of speciation—allopatry and sympatry—lose their meaning if we accept the first statement. Objections to sympatric speciation centered upon the homogenizing force of gene flow. But if demes may be independent in all geographic domains of a species, then sympatry loses its meaning and allopatry its necessity. Independent demes within the central range (sympatric by location) function, in their freedom from gene flow, like the peripheral isolates of allopatric theory. In other words, the terms make no sense outside a theory of population structure that contrasts central panmixia with marginal isolation. They should be abandoned.

3. In this context "sympatric" speciation loses its status as an extremely improbable event. If demes are largely independent, new species may originate anywhere within the geographic range of an ancestral form. Moreover, many evolutionists now doubt that parapatric distributions (far more common then previously thought) must represent cases of secondary contact. White (1978, p. 342) believes that many, if not most, are primary and that speciation can also occur between populations continually in contact if gene flow can be overcome either by strong selection or by the sheer rapidity of potential fixation for major chromosomal variants (see White, 1978, p. 17 on clinal speciation).

4. Most "sympatric" models of speciation are based upon rates and styles of genetic change inconsistent with the reliance placed by the modern synthesis on slow, or at least sequential change.

The most exciting entry among punctuational models for speciation in ecological time is the emphasis, now coming from several quarters, on chromosomal alterations as isolating mechanisms (White 1978; Bush 1975; Carson 1975, 1978; Wilson et al. 1975; Bush et al. 1977)—sometimes called the theory of chromosomal speciation. In certain population structures, particularly in very small and circumscribed groups with high degrees of inbreeding, major chromosomal changes can rise to fixation in less than a handful of generations (mating of heterozygous F_1 sibs to produce F_2 homozygotes for a start).

Allan Wilson, Guy Bush and their colleagues (Wilson et al. 1975; Bush et al. 1977) find a strong correlation between rates of karyotypic and anatomical change, but no relation between amounts of substitution in structural genes and any conventional assessment of phenotypic modification, either in speed or extent. They suggest that speciation may be more a matter of gene regulation and rearrangement than of changes in structural genes that adapt local populations in minor ways to fluctuating environments (the *Biston betularia* model).

Carson (1975, 1978) has also stressed the importance of small demes, chromosomal change, and extremely rapid speciation in his founder-flush theory with its emphasis on extreme bottlenecking during crashes of the flush-crash cycle (see Powell 1978 for experimental support). Explicitly contrasting this view with extrapolationist models based on sequential substitution of structural genes, he writes (1975, p. 88):

> Most theories of speciation are wedded to gradualism, using the mode of origin of intraspecific adaptations as a model . . . I would nevertheless like to propose . . . that speciational events may be set in motion and important genetic saltations towards species formation accomplished by a series of catastrophic, stochastic genetic events . . . initiated when an unusual forced reorganization of the epistatic supergenes of the closed variability system occurs . . . I propose that this cycle of disorganization and reorganization be viewed as the essence of the speciation process.

5. Another consequence of such essentially saltational origin is even more disturbing to conventional views than the rapidity of the process itself, as Carson has forcefully stated. The control of evolution by selection leading to adaptation lies at the heart of the modern synthesis. Thus, reproductive isolation, the definition of speciation, is attained as a by-product of adaptation—that is, a population diverges by sequential adaptation and eventually becomes sufficiently different from its ancestor to foreclose interbreeding. (Selection for reproductive isolation may also be direct when two imperfectly-separate forms come into contact.) But in saltational, chromosomal speciation, reproductive isolation comes first and cannot be considered as an adaptation at all. It is a stochastic event that establishes a species by the technical definition of reproductive isolation. To be sure, the later success of this species in competition may depend upon its subsequent acquisition of adaptations; but the origin itself may be non-adaptive. We can, in fact, reverse the conventional view and argue that speciation, by forming new entities stochastically, provides raw material for selection.

These challenges can be summarized in the claim that a discontinuity in explanation exists between allelic substitutions in local populations (sequential, slow and adaptive) and the origin of new species (often discontinuous and non-adaptive). During the heyday of the modern synthesis, Richard Goldschmidt was castigated for his defense of punctuational speciation. I was told as a graduate student that this great geneticist had gone astray because he had been a lab man with no feel for nature, a person who hadn't studied the adaptation of local populations and couldn't appreciate its potential power, by extrapolation, to form new species. But I discovered, in writing *Ontogeny and Phylogeny,* that Goldschmidt had spent a good part of his career studying geographic variation, largely in the coloration of lepidopteran larvae (where he developed the concept of rate genes to explain minor changes in pattern). I then turned to his major book (1940) and found that his defense of saltational speciation is not based on ignorance of geographic variation, but on an explicit study of it; half the book is devoted to this subject. Goldschmidt concludes that geographic variation is ubiquitous, adaptive, and essential for the persistence of established species. But it is simply not the stuff of speciation; it is a different process. Speciation, Goldschmidt argues, occurs at different rates and uses different kinds of genetic variation. We do not now accept all his arguments about the nature of variation, but his explicit anti-extrapolationist statement is the epitome and foundation of emerging views on speciation discussed in this section. There is a discontinuity in cause and explanation between adaptation in local populations and speciation; they represent two distinct, though interacting, levels of evolution. We might refer to this discontinuity as the *Goldschmidt break,* for he wrote:

> The characters of subspecies are of a gradient type, the species limit is characterized by a gap, an unbridged difference in many characters. This gap cannot be bridged by theoretically continuing the subspecific gradient or cline beyond its actually existing limits. The subspecies do not merge into the species either actually or ideally . . . . Microevolution by accumulation of micromutations—we may also say neo-Darwinian evolution—is a process which leads to diversification strictly within the species, usually, if not exclusively, for the sake of adaptation of the species to specific conditions within the area which it is able to occupy . . . . Subspecies are actually, therefore, neither incipient species nor models for the origin

of species. They are more or less diversified blind alleys within the species. The decisive step in evolution, the first step towards macroevolution, the step from one species to another, requires another evolutionary method than that of sheer accumulation of micromutations (1940, p. 183).

V. Macroevolution and the Wright Break

The extrapolationist model of macroevolution views trends and major transitions as an extension of allelic substitution within populations—the march of frequency distributions through time. Gradual change becomes the normal state of species. The discontinuities of the fossil record are all attributed to its notorious imperfection; the remarkable stasis exhibited by most species during millions of years is ignored (as no data), or relegated to descriptive sections of taxonomic monographs. But gradualism is not the only important implication of the extrapolationist model. Two additional consequences have channeled our concept of macroevolution, both rather rigidly and with unfortunate effect. First, the trends and transitions of macroevolution are envisaged as events in the phyletic mode—populations transforming themselves steadily through time. Splitting and branching are acknowledged to be sure, lest life be terminated by its prevalent extinctions. But splitting becomes a device for the generation of diversity upon designs attained through "progressive" processes of transformation. Splitting, or cladogenesis, becomes subordinate in importance to transformation, or anagenesis (see Ayala 1976, p. 141; but see also Mayr 1963, p. 621 for a rather lonely voice in the defense of copious speciation as an input to "progressive" evolution). Secondly, the adaptationism that prevails in interpreting change in local populations gains greater confidence in extrapolation. For if allelic substitutions in ecological time have an adaptive basis, then surely a unidirectional trend that persists for millions of years within a single lineage cannot bear any other interpretation.

This extrapolationist model of adaptive, phyletic gradualism has been vigorously challenged by several paleobiologists—and again with a claim for discontinuity in explanation at different levels. The general challenge embodies three loosely united themes:

1. Evolutionary trends as a higher level process: Eldredge and I have argued (1972, and Gould and Eldredge 1977) that imperfections of the record cannot explain all discontinuity (and certainly cannot encompass stasis). We regard stasis and discontinuity as an expression of how evolution works when translated into geological time. Gradual change is not the normal state of a species. Large, successful central populations undergo minor adaptive modifications of fluctuating effect through time (Goldschmidt's "diversified blind alleys"), but they will rarely transform *in toto* to something fundamentally new. Speciation, the basis of macroevolution, is a process of branching. And this branching, under any current model of speciation—conventional allopatry to chromosomal saltation—is so rapid in geological translation (thousands of years at most compared with millions for the duration of most fossil species) that its results should generally lie on a bedding plane, not through the thick sedimentary sequence of a long hillslope. (The expectation of gradualism emerges as a kind of double illusion. It represents, first of all, an incorrect translation of conventional allopatry. Allopatric speciation seems so slow and gradual in ecological time that most paleontologists never recognized it as a challenge to the style of gradualism—steady change over millions of years—promulgated by custom as a model for the history of life. But it now appears that "slow" allopatry itself may be less important than a host of alternatives that yield new species rapidly even in ecological time.) Thus, our model of "punctuated equilibria" holds that evolution is concentrated in events of speciation and that successful speciation is an infrequent event punctuating the stasis of large populations that do not alter in fundamental ways during the millions of years that they endure.

But if species originate in geological instants and then do not alter in major ways, then evolutionary trends cannot represent a simple extrapolation of allelic substitution within a population. Trends must be the product of differential success among species (Eldredge and Gould 1972; Stanley 1975). In other words, species themselves must be inputs, and trends the result of their differential origin and survival. Speciation interposes itself as an irreducible level between change in local populations and trends in geological time. Macroevolution is, as Stanley argues (1975, p. 648), decoupled from microevolution.

Sewall Wright recognized the hierarchical implications of viewing species as irreducible inputs to macroevolution when he argued (1967, p. 121) that the relationship between change in local populations and evolutionary trends can only be analogical. Just as mutation is random with respect to the direction of change within a population, so too might speciation be random with respect to the direction of a macroevolutionary trend. A higher form of selection, acting directly upon species through differential rates of extinction, may then be the analog of natural selection working within populations through differential mortality of individuals.

Evolutionary trends therefore represent a third level superposed upon speciation and change within demes. Intrademic events cannot encompass speciation because rates, genetic styles, and relation to adaptation differ for the two processes. Likewise, since trends "use" species as their raw material, they represent a process at a higher level than speciation itself. They reflect a sorting out of speciation events. With apologies for the pun, the hierarchical rupture between speciation and macroevolutionary trends might be called the Wright break.*

As a final point about the extrapolation of methods for the study of events within populations, the cladogenetic basis of macroevolution virtually precludes any direct application of the primary apparatus for microevolutionary theory: classical population genetics. (I believe that essentially all macroevolution is cladogenesis and its concatenated effects. What we call "anagenesis," and often attempt to delineate as a separate phyletic process leading to "progress," is just accumulated cladogenesis filtered through the directing force of species selection (Stanley 1975)—Wright's higher level analog of natural selection. Carson (1978, p. 925) makes the point forcefully, again recognizing Sewall Wright as its long and chief defender:

> Investigation of cladistic events as opposed to phyletic (anagenetic) ones requires a different perspective from that normally assumed in classical population genetics. The statistical and mathematical comfort of the Hardy-Weinberg equilibrium in large populations has to be abandoned in favor of the vague realization that nearly everywhere in nature we are faced with data suggesting the partial or indeed complete sundering of gene pools. If we are to deal realistically with cladogenesis we must seek to delineate each genetic and environmental factor which may promote isolation. The most important devices are clearly those which operate at the very lowest population level: sib from sib, family from family, deme from deme. Formal population genetics just cannot deal with such things, as Wright pointed out long ago.

Eldredge (1979) has traced many conceptual errors and prejudicial blockages to our tendency for conceiving of evolution as the transformation of *characters* within phyletic lineages, rather than as the origin of new *taxa* by cladogenesis (the transformational versus the taxic view in his terms). I believe that, in ways deeper than we realize, our preference for transformational thinking represents a cultural tie to the controlling Western themes of progress and ranking by intrinsic merit—an attitude that can be traced in evolutionary thought to Lamarck's distinction between the march up life's ladder promoted by the *pouvoir de la vie* and the tangential departures imposed by *l'influence des circonstances,* with the first process essential and the second deflective. Nonetheless, macroevolution is fundamentally about the origin of taxa by splitting.

2. The saltational initiation of major transi-

---

* I had the honor—not a word I use frequently, but inescapable in this case—of spending a long evening with Dr. Wright last year. I discovered that his quip about macroevolution, just paraphrased, was no throwaway statement but an embodiment of his deep commitment to a hierarchical view of evolutionary causation. (The failure of many evolutionists to think hierarchically is responsible for the most frequent misinterpretation of Wright's views. He never believed that genetic drift—the Sewall Wright effect as it once was called—is an important agent of evolutionary *change.* He regards it as input to the directional process of interdemic selection for evolution within species. Drift can push a deme off an adaptive peak; selection can then draw it to another peak.

tions: The absence of fossil evidence for intermediary stages between major transitions in organic design, indeed our inability, even in our imagination, to construct functional intermediates in many cases, has been a persistent and nagging problem for gradualistic accounts of evolution. St. George Mivart (1871), Darwin's most cogent critic, referred to it as the dilemma of "the incipient stages of useful structures"—of what possible benefit to a reptile is two percent of a wing? The dilemma has two potential solutions. The first, preferred by Darwinians because it preserves both gradualism and adaptation, is the principle of preadaptation: the intermediary stages functioned in another way but were, by good fortune in retrospect, preadapted to a new role they could play only after greater elaboration. Thus, if feathers first functioned "for" insulation and later "for" the trapping of insect prey (Ostrom 1979), a proto-wing might be built without any reference to flight.

I do not doubt the supreme importance of preadaptation, but the other alternative, treated with caution, reluctance, disdain or even fear by the modern synthesis, now deserves a rehearing in the light of renewed interest in development: perhaps, in many cases, the intermediates never existed. I do not refer to the saltational origin of entire new designs, complete in all their complex and integrated features—a fantasy that would be truly anti-Darwinian in denying any creativity to selection and relegating it to the role of eliminating old models. Instead, I envisage a potential saltational origin for the essential features of key adaptations. Why may we not imagine that gill arch bones of an ancestral agnathan moved forward in one step to surround the mouth and form proto-jaws? Such a change would scarcely establish the *Bauplan* of the gnathostomes. So much more must be altered in the reconstruction of agnathan design—the building of a true shoulder girdle with bony, paired appendages, to say the least. But the discontinuous origin of a proto-jaw might set up new regimes of development and selection that would quickly lead to other, coordinated modifications. Yet Darwin, conflating gradualism with natural selection as he did so often, wrongly proclaimed that any such discontinuity, even for organs (much less taxa) would destroy his theory:

> If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down (1859, p. 189).

During the past 30 years, such proposals have generally been treated as a fantasy signifying surrender—an invocation of hopeful monsters rather than a square facing of a difficult issue. But our renewed interest in development, the only discipline of biology that might unify molecular and evolutionary approaches into a coherent science, suggests that such ideas are neither fantastic, utterly contrary to genetic principles, nor untestable.

Goldschmidt conflated two proposals as causes for hopeful monsters—"systemic mutations" involving the entire genome (a spinoff from his fallacious belief that the entire genome acted as an integrated unit), and small mutations with large impact upon adult phenotypes because they work upon early stages of ontogeny and lead to cascading effects throughout embryology. We reject his first proposal, but the second, eminently plausible, theme might unite a Darwinian insistence upon continuity of genetic change with a macroevolutionary suspicion of phenetic discontinuity. It is, after all, a major focus in the study of heterochrony (effects, often profound, of small changes in developmental rate upon adult phenotypes); it is also implied in the emphasis now being placed upon regulatory genes in the genesis of macroevolutionary change (King and Wilson 1975)—for regulation is fundamentally about timing in the complex orchestration of development. Moreover, although we cannot readily build "hopeful monsters," the subject of major change through alteration of developmental rate can be treated, perhaps more than analogically, both by experiment and comparative biology. The study of spontaneous anomalies of development (teratology) and experimental perturbations of embryogenic rates explores the tendencies and boundaries of developmental systems and allows us to specify potential pathways of macroevolutionary change (see, for example, the stunning experiment of Hampé 1959, on recreation of reptilian patterns in birds, after 200 million years of their phenotypic absence, by experimental manipulations that amount to alterations in rate of development for the fibula). At the very least, these approaches work with real information and seem so much more fruitful than the construction of adaptive stories or the invention of hypothetical intermediates.

3. The importance of non-adaptation: The emphasis on natural selection as the only directing force of any importance in evolution led inevitably to an analysis of all attributes of organisms as adaptations. Indeed, the tendency has infected our language, for, without thinking about what it implies, we use "adaptation" as our favored, *descriptive* term for designating any recognizable bit of changed morphology in evolution. I believe that this "adaptationist program" has had decidedly unfortunate effects in biology (Gould and Lewontin, 1979). It has led to a reliance on speculative storytelling in preference to the analysis of form and its constraints; and, if wrong, in any case, it is virtually impossible to dislodge because the failure of one story leads to invention of another rather than abandonment of the enterprise.

Yet, as I argued earlier, the hegemony of adaptation has been broken at the two lower levels of our evolutionary hierarchy: variation within populations, and speciation. Most populations may contain too much variation for selection to maintain; moreover, if the neutralists are even part right, much allelic substitution occurs without controlling influence from selection, and with no direct relationship to adaptation. If species often form as a result of major chromosomal alterations, then their origin—the establishment of reproductive isolation—may require no reference to adaptation. Similarly, at this third level of macroevolution, both arguments previously cited against the conventional extrapolationist view require that we abandon strict adaptationism.

i) If trends are produced by the unidirectional transformation of populations (orthoselection), then they can scarcely receive other than a conventional adaptive explanation. After all, if adaptation lies behind single allelic substitutions in the *Biston betularia* model for change in local populations, what else but even stronger, more persistent selection and adaptive orientation can render a trend that persists for millions of years? But if trends represent a higher-level process of differential origin and mortality among species, then a suite of potentially non-adaptive explanations must be considered. Trends, for example, may occur because some kinds of species tend to speciate more often than others. This tendency may reside in the character of environments or in attributes of behavior and population structure bearing no relationship to morphologies that spread through lineages as a result of higher speciation rates among some of their members. Or trends may arise from the greater longevity of certain kinds of species. Again, this greater persistence may have little to do with the morphologies that come to prevail as a result. I suspect that many morphological trends in paleontology—a bugbear of the profession because we have been unable to explain them in ordinary adaptive terms—are non-adaptive sequelae of differential species success based upon environments and population structures.

ii) If transitions represent the continuous and gradual transformation of populations, then they must be regulated by adaptation throughout (even though adaptive orientation may alter according to the principle of preadaptation). But if discontinuity arises through shifts in development, then directions of potential change may be limited and strongly constrained by the inherited program and developmental mechanics of an organism. Adaptation may determine whether or not a hopeful monster survives, but primary constraint upon its genesis and direction resides with inherited ontogeny, not with selective modelling.

VI. Quo Vadis?

My crystal ball is clouded both by the dust of these growing controversies and by the mists of ignorance emanating from molecular biology, where even the basis of regulation in eukaryotes remains shrouded in mystery. I think I can see what is breaking down in evolutionary theory—the strict construction of the modern synthesis with its belief in pervasive adaptation, gradualism, and extrapolation by smooth continuity from causes of change in local populations to major trends and transitions in the history of life. I do not know what will take its place as a unified theory, but I would venture to predict some themes and outlines.

The new theory will be rooted in a hierarchical view of nature. It will not embody the depressing notion that levels are fundamentally distinct and necessarily opposed to each other in their identification of causes (as the older paleontologists held in maintaining that macroevolution could not, in principle, be referred to the same causes that regulate microevolution—e.g., Osborn 1922). It will possess a common body of causes and constraints, but will recognize that they work in characteristically different ways upon the material of different levels—intrademic change, speciation, and patterns of macroevolution.

As its second major departure from current orthodoxy, the new theory will restore to biology a concept of organism. In an exceedingly curious and unconscious bit of irony, strict selectionism (which was not, please remember, Darwin's own view) debased what had been a mainstay of biology—the organism as an integrated entity exerting constraint over its history. St. George Mivart expressed the subtle point well in borrowing a metaphor from Galton. I shall call it Galton's polyhedron. Mivart writes (1871, pp. 228–229):

> This conception of such internal and latent capabilities is somewhat like that of Mr. Galton . . . according to which the organic world consists of entities, each of which is, as it were, a spheroid with many facets on its surface, upon one of which it reposes in stable equilibrium. When by the accumulated action of incident forces this equilibrium is disturbed, the spheroid is supposed to turn over until it settles on an adjacent facet once more in stable equilibrium. The internal tendency of an organism to certain considerable and definite changes would correspond to the facets on the surface of the spheroid.

Under strict selectionism, the organism is a sphere. It exerts little constraint upon the character of its potential change; it can roll along all paths. Genetic variation is copious, small in its increments, and available in all directions—the essence of the term "random" as used to guarantee that variation serves as raw material only and that selection controls the direction of evolution.

By invoking Galton's polyhedron, I recommend no return to the antiquated and anti-Darwinian view that mysterious "internal" factors provide direction inherently, and that selection only eliminates the unfit (orthogenesis, various forms of vitalism and finalism). Instead, the facets are constraints exerted by the developmental integration of organisms themselves. Change cannot occur in all directions, or with any increment; the organism is not a metaphorical sphere. When the polyhedron tumbles, selection may usually be the propelling force. But if adjacent facets are few in number and wide in spacing, then we cannot identify selection as the only, or even the primary control upon evolution. For selection is channeled by the form of the polyhedron it pushes, and these constraints may exert a more powerful influence upon evolutionary directions than the external push itself. This is the legitimate sense of a much maligned claim that "internal factors" are important in evolution. They channel and constrain Darwinian forces; they do not stand in opposition to them. Most of the other changes in evolutionary viewpoint that I have advocated throughout this paper fall out of Galton's metaphor: punctuational change at all levels (the flip from facet to facet, since homeostatic systems change by abrupt shifting to new equilibria); essential non-adaptation, even in major parts of the phenotype (change in an integrated organism often has effects that reverberate throughout the system); channeling of direction by constraints of history and developmental architecture. Organisms are not billiard balls, struck in deterministic fashion by the cue of natural selection, and rolling to optimal positions on life's table. They influence their own destiny in interesting, complex, and comprehensible ways. We must put this concept of organism back into evolutionary biology.

Literature Cited

Ayala, F. J. 1976. Molecular genetics and evolution. Pp. 1–20. In: Ayala, F. J., ed. Molecular Evolution. Sinauer Associates; Sunderland, Mass.

Bateson, G. 1978. Mind and Nature. E. P. Dutton; New York.

Bush, G. L. 1975. Modes of animal speciation. Annu. Rev. Ecol. Syst. *6*:339–364.

Bush, G. L., S. M. Case, A. C. Wilson, and J. L. Patton. 1977. Rapid speciation and chromosomal evolution in mammals. Proc. Nat. Acad. Sci. *74*:3942–3946.

Carson, H. L. 1975. The genetics of speciation at the diploid level. Am. Nat. *109*:83–92.

CARSON, H. L. 1978. Chromosomes and species formation. Evolution. *32*:925–927.

DARWIN, C. 1859. On the Origin of Species. 490 pp. John Murray; London.

DARWIN, C. 1880. Sir Wyville Thomson and natural selection. Nature *23*:32.

DOBZHANSKY, TH. 1937. Genetics and the Origin of Species. 364 pp. Columbia Univ. Press; New York.

DOBZHANSKY, TH. 1951. Genetics and the Origin of Species. (3rd ed.). 364 pp. Columbia Univ. Press; New York.

EHRLICH, P. R. AND P. H. RAVEN. 1969. Differentiation of populations. Science. *165*:1228–1232.

ELDREDGE, N. 1979. Alternative approaches to evolutionary theory. Bull. Carnegie Mus. Nat. Hist. pp. 7–19.

ELDREDGE, N. AND J. CRACRAFT. 1980. Phylogenetic Patterns and the Evolutionary Process. Columbia Univ. Press; New York.

ELDREDGE, N. AND S. J. GOULD. 1972. Punctuated equilibria: An alternative to phyletic gradualism. Pp. 82–115. In: Schopf, T. J. M., ed. Models in Paleobiology. Freeman, Cooper and Co.; San Francisco, California.

GOLDSCHMIDT, R. 1940. The Material Basis of Evolution. 436 pp. Yale Univ. Press; New Haven, Conn.

GOULD, S. J. 1980. G. G. Simpson, paleontology and the modern synthesis. In: Mayr, E., ed. Conference on the making of the Modern Synthesis. Harvard Univ. Press; Cambridge, Mass.

GOULD, S. J. AND N. ELDREDGE. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. Paleobiology. *3*:115–151.

GOULD, S. J. AND R. C. LEWONTIN. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist program. Proc. R. Soc. London. *205*:581–598.

HAMPÉ, A. 1959. Contribution à l'étude du développement et de la regulation des déficiences et des excédents dans la patte de l'embryon de poulet. Arch. Anat. Microsc. Morphol. Exp. *48*:345–478.

KING, M. C. AND A. C. WILSON. 1975. Evolution at two levels in humans and chimpanzees. Science. *188*:107–116.

KOESTLER, A. 1978. Janus: a Summing Up. Random House; New York.

LEWONTIN, R. C. 1974. The Genetic Basis of Evolutionary Change. 346 pp. Columbia Univ. Press; New York.

LEWONTIN, R. C. AND J L. HUBBY. 1966. A molecular approach to the study of genic heterozygosity in natural populations. II. Amount of variation and degree of heterozygosity in natural populations of *Drosophila pseudoobscura*. Genetics. *54*:595–609.

MAYR, E. 1942. Systematics and the Origin of Species. 334 pp. Columbia Univ Press; New York.

MAYR, E. 1963. Animal Species and Evolution. 797 pp. Belknap Press of Harvard Univ. Press; Cambridge, Mass.

MIVART, ST. G. 1871. On the Genesis of Species. 296 pp. MacMillan; London.

NEI, M. 1975. Molecular Population Genetics and Evolution. American Elsevier; New York.

OSBORN, H. F. 1922. Orthogenesis as observed from paleontological evidence beginning in the year 1889. Am. Nat. *56*:134–143.

OSTROM, J H. 1979. Bird flight: How did it begin. Am. Sci. *67*:46–56.

POWELL, J. R. 1978. The founder-flush speciation theory: an experimental approach. Evolution. *32*:465–474.

ROBSON, G. C. AND O. W. RICHARDS. 1936. The Variation of Animals in Nature. Longmans, Green, and Co.; London.

ROMANES, G. J. 1900. Darwin and after Darwin, vol. 2. Post-Darwinian questions. Heredity and Utility. 344 pp. Longmans, Green, and Co.; London.

SIMPSON, G. G. 1944. Tempo and Mode in Evolution. 237 pp. Columbia Univ. Press; New York.

SIMPSON, G. G. 1953. The Major Features of Evolution. 434 pp. Columbia Univ. Press; New York.

STANLEY, S. M. 1975. A theory of evolution above the species level. Proc. Nat. Acad. Sci. *72*:646–650.

WHITE, M. J. D. 1978. Modes of Speciation. 455 pp. W.H. Freeman; San Francisco, California.

WILSON, A. C., G. L. BUSH, S. M. CASE, AND M. C. KING. 1975. Social structuring of mammalian populations and rate of chromosomal evolution. Proc. Nat. Acad. Sci. *72*:5061–5065.

WILSON, A. C., S. S. CARLSON, AND T. J. WHITE. 1977. Biochemical evolution. Annu. Rev. Biochem. *46*:573–639.

WILSON, E. O. ET AL. 1973. Life on Earth. Sinauer Associates; Sunderland, Mass.

WRIGHT, S. 1967. Comments on the preliminary working papers of Eden and Waddington. In: Moorehead, P. S. and M. M. Kaplan, eds. Mathematical Challenges to the Neo-Darwinian Theory of Evolution. Wistar Inst. Symp. *5*:117–120.