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Darwinism and the Expansion of Evolutionary Theory

Stephen Jay Gould

Ben Sira, author of the apocryphal book of Ecclesiasticus, paid homage to the heroes of Israel in a noted passage beginning, "let us now praise famous men." He glorified great teachers above all others, for their fame shall eclipse the immediate triumphs of kings and conquerors. And he argued that the corporeal death of teachers counts for nothing—indeed, it should be celebrated—since great ideas must live forever: "His name will be more glorious than a thousand others, and if he dies, that will satisfy him just as well." These sentiments express the compulsion we feel to commemorate the deaths of great thinkers; for their ideas still direct us today. Charles Darwin died 100 years ago, on 19 April 1882, but his name still causes fundamentalists to shudder and scientists to draw battle lines amidst their accolades.

What Is Darwinism?

Darwin often stated that his biological work had embodied two different goals (1): to establish the fact of evolution, and to propose natural selection as its primary mechanism. "I had," he wrote, "two distinct objects in view; firstly to show that species had not been separately created, and secondly, that natural selection had been the chief agent of change" (2).

Although "Darwinism" has often been equated with evolution itself in popular literature, the term should be restricted to the body of thought allied with Darwin's own theory of mechanism, his second goal. This decision does not provide an unambiguous definition, if only because Darwin himself was a pluralist who granted pride of place to natural selection, but also advocated an

important role for Lamarckian and other nonselectionist factors. Thus, as the 19th century drew to a close, G. J. Romanes and A. Weismann squared off in a terminological battle for rights to the name "Darwinian"—Romanes claiming it for his eclectic pluralism, Weismann for his strict selectionism (3).

If we agree, as our century generally has, that "Darwinism" should be restricted to the world view encompassed by the theory of natural selection itself, the problem of definition is still not easily resolved. Darwinism must be more than the bare bones of the mechanics: the principles of superfecundity and inherited variation, and the deduction of natural selection therefrom. It must, fundamentally, make a claim for wide scope and dominant frequency; natural selection must represent the primary directing force of evolutionary change.

I believe that Darwinism, under these guidelines, can best be defined as embodying two central claims and a variety of peripheral and supporting statements more or less strongly tied to the central postulates; Darwinism is not a mathematical formula or a set of statements, deductively arranged.

1) The creativity of natural selection. Darwinians cannot simply claim that natural selection operates since everyone,

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including Paley and the natural theologians, advocated selection as a device for removing unfit individuals at both extremes and preserving, intact and forever, the created type (4). The essence of Darwinism lies in a claim that natural selection is the primary directing force of evolution, in that it creates fitter phenotypes by differentially preserving, generation by generation, the best adapted organisms from a pool of random variants (5) that supply raw material only, not direction itself. Natural selection is a creator; it builds adaptation step by step.

Darwin's contemporaries understood that natural selection hinged on the argument for creativity. Natural selection can only eliminate the unfit, his opponents proclaimed; something else must create the fit. Thus, the American Neo-Lamarckian E. D. Cope wrote a book with the sardonic title *The Origin of the Fittest* (6), and Charles Lyell complained to Darwin that he could understand how selection might operate like two members of the "Hindoo triad"—Vishnu the preserver and Siva the destroyer—but not like Brahma the creator (7).

The claim for creativity has important consequences and prerequisites that also become part of the Darwinian corpus. Most prominently, three constraints are imposed on the nature of genetic variation (or at least the evolutionarily significant portion of it). (i) It must be copious since selection makes nothing directly and requires a large pool of raw material. (ii) It must be small in scope. If new species characteristically arise all at once, then the fit are formed by the process of variation itself, and natural selection only plays the negative role of executioner for the unfit. True saltationist theories have always been considered anti-Darwinian on this basis. (iii) It must be undirected. If new environments can elicit heritable, adaptive variation, then creativity lies in the process of variation, and selection only eliminates the unfit. Lamarckism is an anti-Darwinian theory because it advocates directed variation; organisms perceive felt needs, adapt their bodies accordingly, and pass these modifications directly to offspring.

Two additional postulates, generally considered part and parcel of the Darwinian world view, are intimately related to the claim for creativity, but are not absolute prerequisites or necessary deductive consequences: (i) *Gradualism*. If creativity resides in a step-by-step process of selection from a pool of random variants, then evolutionary change must be dominantly continuous and descend-

ants must be linked to ancestors by a long chain of smoothly intermediate phenotypes. Darwin's own gradualism precedes his belief in natural selection and has deeper roots (8); it dominated his world view and provided a central focus for most other theories that he proposed, including the origin of coral atolls by subsidence of central islands, and formation of vegetable mold by earthworms (9, 10). (ii) *The adaptationist program*. If selection becomes creative by superin-

but . . . (13, p. 62). Darwin developed his theory of natural selection by transferring the basic argument of Adam Smith's economics into nature (14): an ordered economy can best be achieved by letting individuals struggle for personal profits, thereby permitting a natural sifting of the most competitive (*laissez-faire*); an ordered ecology is a transient balance established by successful competitors pursuing their own Darwinian edge.

Summary. The essence of Darwinism lies in the claim that natural selection is a creative force, and in the reductionist assertion that selection upon individual organisms is the locus of evolutionary change. Critiques of adaptationism and gradualism call into doubt the traditional consequences of the argument for creativity, while a concept of hierarchy, with selection acting upon such higher-level "individuals" as demes and species, challenges the reductionist claim. An expanded hierarchical theory would not be Darwinism, as strictly defined, but it would capture, in abstract form, the fundamental feature of Darwin's vision—direction of evolution by selection at each level.

tending, generation by generation, the continuous incorporation of favorable variation into altered forms, then evolutionary change must be fundamentally adaptive. If evolution were saltational, or driven by internally generated biases in the direction of variation, adaptation would not be a necessary attribute of evolutionary change.

The argument for creativity rests on relative frequency, not exclusivity. Other factors must regulate some cases of evolutionary change—randomness as a direct source of modification, not only of raw material, for example. The Darwinian strategy does not deny other factors, but attempts to circumscribe their domain to few and unimportant cases.

2) Selection operates through the differential reproductive success of individual organisms (the "struggle for existence" in Darwin's terminology). Selection is an interaction among individuals; there are no higher-order laws in nature, no statements about the "good" of species or ecosystems. If species survive longer, or if ecosystems appear to display harmony and balance, these features arise as a by-product of selection among individuals for reproductive success.

Although evolutionists, including many who call themselves Darwinians, have often muddled this point (11), it is a central feature of Darwin's logic (12). It underlies all his colorful visual imagery including the metaphor of the wedge (13, p. 67), or the true struggle that underlies an appearance of harmony: "we behold the face of nature bright with gladness,"

As a primary consequence, this focus upon individual organisms leads to reductionism, not to ultimate atoms and molecules of course, but of higher-order, or macroevolutionary, processes to the accumulated struggles of individuals. Extrapolationism is the other side of the same coin—the claim that natural selection within local populations is the source of all important evolutionary change.

Darwinism and the Modern Synthesis

Although Darwin succeeded in his first goal, and lies in Westminster Abbey for his success in establishing the fact of evolution, his theory of natural selection did not triumph as an orthodoxy until long after his death. The Mendelian component to the modern, or Neo-Darwinian, theory only developed in our century. Moreover, and ironically, the first Mendelians emphasized macromutations and were non-Darwinians on the issue of creativity as discussed above.

The Darwinian resurgence began in earnest in the 1930's, but did not crystallize until the 1950's. At the last Darwinian centennial, in 1959 (both the 100th anniversary of the *Origin of Species* and the 150th of Darwin's birth), celebrations throughout the world lauded the "modern synthesis" as Darwinism finally triumphant (15).

Julian Huxley, who coined the term (16), defined the "modern synthesis" as an integration of the disparate parts of biology about a Darwinian core (17).

Synthesis occurred at two levels: (i) The Mendelian research program merged with Darwinian traditions of natural history, as Mendelians recognized the importance of micromutations and their correspondence with Darwinian variation, and as population genetics supplied a quantitative mechanics for evolutionary change. (ii) The traditional disciplines of natural history, systematics, paleontology, morphology, and classical botany, for example (18), were integrated within the Darwinian core, or at least rendered consistent with it.

The initial works of the synthesis, particularly Dobzhansky's first (1937) edition of *Genetics and the Origin of Species*, were not firmly Darwinian (as defined above), and did not assert a dominant frequency for natural selection. They were more concerned with demonstrating that large-scale phenomena of evolution are consistent with the principles of genetics, whether Darwinian or not; and they therefore, for example, granted greater prominence to genetic drift than later editions of the same works would allow.

Throughout the late 1940's and 1950's, however, the synthesis hardened about its Darwinian core. Analysis of textbooks and, particularly, the comparison of first with later editions of the founding documents, demonstrates the emergence of natural selection and adaptation as preeminent factors of evolution. Thus, for example, G. G. Simpson redefined "quantum evolution" in 1953 as a limiting rate for adaptive phyletic transformation, not, as he had in 1944, as a higher-order analog of genetic drift, with a truly inadaptable phase between stabilized end points (19). Dobzhansky removed chapters and reduced emphasis upon rapid modification and random components to evolutionary change (20). David Lack reassessed his work on Darwin's finches and decided that minor differences among species are adaptive after all (21). His preface to the 1960 reissue of his monograph features the following statement (22):

This text was completed in 1944 and . . . views on species-formation have advanced. In particular, it was generally believed when I wrote the book that, in animals, nearly all of the differences between subspecies of the same species, and between closely related species in the same genus, were without adaptive significance. . . . Sixteen years later, it is generally believed that all, or almost all, subspecific and specific differences are adaptive. . . . Hence it now seems probable that at least most of the seemingly non-adaptive differences in Darwin's finches would, if more were known, prove to be adaptive.

Mayr's definition of the synthesis, offered without rebuttal at a conference of historians and architects of the theory, reflects this crystallized version:

The term "evolutionary synthesis" was introduced by Julian Huxley . . . to designate the general acceptance of two conclusions: gradual evolution can be explained in terms of small genetic changes ("mutations") and recombination, and the ordering of this genetic variation by natural selection; and the observed evolutionary phenomena, particularly macro-evolutionary processes and speciation, can be explained in a manner that is consistent with the known genetic mechanisms (23).

This definition restates the two central claims of Darwinism discussed in the last section: Mayr's first conclusion, with its emphasis on gradualism, small genetic change, and natural selection, represents the argument for creativity; while the second embodies the claim for reduction. I have been challenged for erecting a straw man in citing this definition of the synthesis (24), but it was framed by a man who is both an architect and the leading historian of the theory, and it is surely an accurate statement of what I was taught as a graduate student in the mid-1960's. Moreover, these very words have been identified as the "broad version" of the synthesis (as opposed to a more partisan and restrictive stance) by White (25), a leading evolutionist and scholar who lived through it all.

The modern synthesis has sometimes been so broadly construed, usually by defenders who wish to see it as fully adequate to meet and encompass current critiques, that it loses all meaning by including everything. If, as Stebbins and Ayala claim, "selectionist" and "neutralist" views of molecular evolution are competing hypotheses within the framework of the synthetic theory of evolution" (26), then what serious views are excluded? King and Jukes, authors of the neutralist theory, named it "non-Darwinian evolution" in the title of their famous paper (27). Stebbins and Ayala have tried to win an argument by redefinition. The essence of the modern synthesis must be its Darwinian core. If most evolutionary change is neutral, the synthesis is severely compromised.

What Is Happening to Darwinism

Current critics of Darwinism and the modern synthesis are proposing a good deal more than a comfortable extension of the theory, but much less than a revolution. In my partisan view, neither of Darwinism's two central themes will survive in their strict formulation; in that

sense, "the modern synthesis, as an exclusive proposition, has broken down on both of its fundamental claims" (28). However, I believe that a restructured evolutionary theory will embody the essence of the Darwinian argument in a more abstract, and hierarchically extended form. The modern synthesis is incomplete, not incorrect.

Critique of Creativity: Gradualism

At issue is not the general idea that natural selection can act as a creative force; the basic argument, in principle, is a sound one. Primary doubts center on the subsidiary claims—gradualism and the adaptationist program. If most evolutionary changes, particularly large-scale trends, include major nonadaptive components as primary directing or channeling features, and if they proceed more in an episodic than a smoothly continuous fashion, then we inhabit a different world from the one Darwin envisaged.

Critiques of gradualist thought proceed on different levels and have different import, but none are fundamentally opposed to natural selection. They are therefore not directed against the heart of Darwinian theory, but against a fundamental subsidiary aspect of Darwin's own world view—one that he consistently conflated with natural selection, as in the following famous passage: "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" (29).

At the levels of microevolution and speciation, the extreme saltationist claim that new species arise all at once, fully formed, by a fortunate macromutation would be anti-Darwinian, but no serious thinker now advances such a view, and neither did Richard Goldschmidt (30), the last major scholar to whom such an opinion is often attributed. Legitimate claims range from the saltational origin of key features by developmental shifts of dissociable segments of ontogeny (31) to the origin of reproductive isolation (speciation) by major and rapidly incorporated genetic changes that precede the acquisition of adaptive, phenotypic differences (32).

Are such styles of evolution anti-Darwinian? What can one say except "yes and no." They do not deny a creative role to natural selection, but neither do they embody the constant superintending of each event, or the step-by-step construction of each major feature, that

traditional views about natural selection have advocated. If new *Baupläne* often arise in an adaptive cascade following the saltational origin of a key feature, then part of the process is sequential and adaptive, and therefore Darwinian; but the initial step is not, since selection does not play a creative role in building the key feature. If reproductive isolation often precedes adaptation, then a major aspect of speciation is Darwinian (for the new species will not prosper unless it builds distinctive adaptations in the sequential mode), but its initiation, including the defining feature of reproductive isolation, is not.

At the macroevolutionary level of trends, the theory of punctuated equilibrium (33) proposes that established species generally do not change substantially in phenotype over a lifetime that may encompass many million years (stasis), and that most evolutionary change is concentrated in geologically instantaneous events of branching speciation. These geological instants, resolvable (34) in favorable stratigraphic circumstances (so that the theory can be tested for its proposed punctuations as well as for its evident periods of stasis), represent amounts of microevolutionary time fully consistent with orthodox views about speciation. Indeed, Eldredge and I originally proposed punctuated equilibrium as the expected geological consequence of Mayr's theory of peripatric speciation. The non-Darwinian implications of punctuated equilibrium lie in its suggestions for the explanation of evolutionary trends (see below), not in the tempo of individual speciation events. Although punctuated equilibrium is a theory for a higher level of evolutionary change, and must therefore be agnostic with respect to the role of natural selection in speciation, the world that it proposes is quite different from that traditionally viewed by paleontologists (and by Darwin himself) as the proper geological extension of Darwinism.

The "gradualist-punctationalist debate," the general label often applied to this disparate series of claims, may not be directed at the heart of natural selection, but it remains an important critique of the Darwinian tradition. The world is not inhabited exclusively by fools, and when a subject arouses intense interest and debate, as this one has, something other than semantics is usually at stake. In the largest sense, this debate is but one small aspect of a broader discussion about the nature of change: Is our world (to construct a ridiculously oversimplified dichotomy) primarily one of con-

stant change (with structure as a mere incarnation of the moment), or is structure primary and constraining, with change as a "difficult" phenomenon, usually accomplished rapidly when a stable structure is stressed beyond its buffering capacity to resist and absorb. It would be hard to deny that the Darwinian tradition, including the modern synthesis, favored the first view while "punctationalist" thought in general, including such aspects of classical morphology as D'Arcy Thompson's theory of form (35), prefers the second.

Critique of Creativity: Adaptation

The primary critiques of adaptation have arisen from molecular data, particularly from the approximately even ticking of the molecular clock, and the argument that natural populations generally maintain too much genetic variation to explain by natural selection, even when selection acts to preserve variation as in, for example, heterozygote advantage and frequency-dependent selection. To these phenomena, Darwinians have a response that is, in one sense, fully justified: Neutral genetic changes without phenotypic consequences are invisible to Darwinian processes of selection upon organisms and therefore represent a legitimate process separate from the subjects that Darwinism can treat. Still, since issues in natural history are generally resolved by appeals to relative frequency, the domain of Darwinism is restricted by these arguments.

But another general critique of the adaptationist program has been reasserted within the Darwinian domain of phenotypes (36). The theme is an old one, and not unfamiliar to Darwinians. Darwin himself took it seriously, as did the early, pluralistic accounts of the modern synthesis. The later, "hard" version of the synthesis relegated it to unimportance or lip service. The theme is two-pronged, both arguments asserting that the current utility of a structure permits no assumption that selection shaped it. First, the constraints of inherited form and developmental pathways may so channel any change that even though selection induces motion down permitted paths, the channel itself represents the primary determinant of evolutionary direction. Second, current utility permits no necessary conclusion about historical origin. Structures now indispensable for survival may have arisen for other reasons and been "coopted" by functional shift for their new role.

Both arguments have their Darwinian versions. First, if the channels are set by past adaptations, then selection remains preeminent, for all major structures are either expressions of immediate selection, or channeled by a phylogenetic heritage of previous selection. Darwin struggled mightily with this problem. Ultimately, in a neglected passage that I regard as one of the most crucial paragraphs in the *Origin of Species* (37), he resolved his doubts, and used this argument to uphold the great British tradition of adaptationism. Second, if coopted structures initially arose as adaptations for another function, then they too are products of selection, albeit in a regime not recorded by their current usage. We call this phenomenon preadaptation; as the primary solution to Mivart's taunt (38) about "the incipient stages of useful structures," it is a central theme of orthodox Darwinism.

But both arguments also have non-Darwinian versions, not widely appreciated but potentially fundamental. First, many features of organic architecture and developmental pathways have never been adaptations to anything, but arose as by-products or incidental consequences of changes with a basis in selection. Seilacher has suggested, for example, that the divaricate pattern of molluscan ornamentation may be nonadaptive in its essential design. In any case, it is certainly a channel for some fascinating subsidiary adaptations (39). Second, many structures available for cooption did not arise as adaptations for something else (as the principle of preadaptation assumes) but were nonadaptive in their original construction. Evolutionary morphology now lacks a term for these coopted structures, and unnamed phenomena are not easily conceptualized. Vrba and I suggest that they be called exaptations (40), and present a range of potential examples from the genitalia of hyenas to redundant DNA.

Evolutionists admit, of course, that all selection yields by-products and incidental consequences, but we tend to think of these nonadaptations as a sort of evolutionary frill, a set of small and incidental modifications with no major consequences. I dispute this assessment and claim that the pool of nonadaptations must be far greater in extent than the direct adaptations that engender them. This pool must act as a higher-level analog of genetic variation, as a phenotypic source of raw material for further evolution. Nonadaptations are not just incidental allometric and pleiotropic effects on other parts of the body,

but multifarious expressions potentially within any adapted structure. No one doubts, for example, that the human brain became large for a set of complex reasons related to selection. But, having reached its unprecedented bulk, it could, as a computer of some sophistication, perform in an unimagined range of ways bearing no relation to the selective reasons for initial enlargement. Most of human society may rest on these nonadaptive consequences. How many human institutions, for example, owe their shape to that most terrible datum that intelligence permitted us to grasp—the fact of our personal mortality.

I do not claim that a new force of evolutionary change has been discovered. Selection may supply all immediate direction, but if highly constraining channels are built of nonadaptations, and if evolutionary versatility resides primarily in the nature and extent of nonadaptive pools, then “internal” factors of organic design are an equal partner with selection. We say that mutation is the ultimate source of variation, yet we grant a fundamental role to recombination and the evolution of sexuality—often as a prerequisite to multicellularity, the Cambrian explosion and, ultimately, us. Likewise, selection may be the ultimate source of evolutionary change, but most actual events may owe more of their shape to its nonadaptive sequelae.

Is Evolution a Product of Selection Among Individuals?

Although arguments for a multiplicity of units of selection have been advanced and widely discussed (41), evolutionists have generally held fast to the overwhelming predominance, if not exclusivity, of organisms as the objects sorted by selection—Dawkins’ (42) attempt at further reduction to the gene itself notwithstanding. How else can we explain the vehement reaction of many evolutionists to Wynne-Edwards’ theory of group selection for the maintenance of altruistic traits (43), or the delight felt by so many when the same phenomena were explained, under the theory of kin selection, as a result of individuals pursuing their traditional Darwinian edge. I am not a supporter of Wynne-Edwards’ particular hypothesis, nor do I doubt the validity and importance of kin selection; I merely point out that the vehemence and delight convey deeper messages about general attitudes.

Nonetheless, I believe that the traditional Darwinian focus on individual bodies, and the attendant reductionist

account of macroevolution, will be supplanted by a hierarchical approach recognizing legitimate Darwinian individuals at several levels of a structural hierarchy, including genes, bodies, demes, species, and clades.

The argument may begin with a claim that first appears to be merely semantic, yet contains great utility and richness in implication, namely the conclusion advanced by Ghiselin and later supported by Hull that species should be treated as individuals, not as classes (44). Most species function as entities in nature, with coherence and stability. And they display the primary characteristics of a Darwinian actor; they vary within their population (clade in this case), and they exhibit differential rates of birth (speciation) and death (extinction).

Our language and culture include a prejudice for applying the concept of individual only to bodies, but any coherent entity that has a unique origin, sufficient temporal stability, and a capacity for reproduction with change can serve as an evolutionary agent. The actual hierarchy of our world is a contingent fact of history, not a heuristic device or a logical necessity. One can easily imagine a world devoid of such hierarchy, and conferring the status of evolutionary individual upon bodies alone. If genes could not duplicate themselves and disperse among chromosomes, we might lack the legitimately independent level that the “selfish DNA” hypothesis establishes for some genes (45). If new species usually arose by the smooth transformation of an entire ancestral species, and then changed continuously toward a descendant form, they would lack the stability and coherence required for defining evolutionary individuals. The theory of punctuated equilibrium allows us to individuate species in both time and space; this property (rather than the debate about evolutionary tempo) may emerge as its primary contribution to evolutionary theory.

In itself, individuation does not guarantee the strong claim for evolutionary agency: that the higher-level individual acts as a unit of selection in its own right. Species might be individuals, but their differential evolutionary success might still arise entirely from natural selection acting upon their parts, that is, upon phenotypes of organisms. A trend toward increasing brain size, for example, might result from the greater longevity of big-brained species. But big-brained species might prosper only because the organisms within them tend to prevail in traditional competition.

But individuation of higher-level units

is enough to invalidate the reductionism of traditional Darwinism—for pattern and style of evolution depend critically on the disposition of higher-level individuals, even when all selection occurs at the traditional level of organisms. Sewall Wright, for example, has often spoken of “interdemic selection” in his shifting balance theory (46), but he apparently uses this phrase in a descriptive sense and believes that the mechanism of change usually resides in selection among individual organisms, as when, for example, migrants from one deme swamp another. Still, the fact of deme structure itself—that is, the individuation of higher-level units within a species—is crucial to the operation of shifting balance. Without division into demes, and under panmixia, genetic drift could not operate as the major source of variation required by the theory.

We need not, however, confine ourselves to the simple fact of individuation as an argument against Darwinian reductionism. For the strong claim that higher-level individuals act as units of selection in their own right can often be made. Many evolutionary trends, for example, are driven by differential frequency of speciation (the analog of birth) rather than by differential extinction (the more usual style of selection by death). Features that enhance the frequency of speciation are often properties of populations, not of individual organisms, for example, dependence of dispersal (and resultant possibilities for isolation and speciation) on size and density of populations.

Unfortunately, the terminology of this area is plagued with a central confusion (some, I regret to say, abetted by my own previous writings). Terms like “interdemic selection” or “species selection” (47) have been used in the purely descriptive sense, when the sorting out among higher-level individuals may arise solely from natural selection operating upon organisms. Such cases are explained by Darwinian selection, although they are irreducible to organisms alone. The same terms have been restricted to cases of higher-level individuals acting as units of selection. Such situations are non-Darwinian, and irreducible on this strong criterion. Since issues involving the locus of selection are so crucial in evolutionary theory, I suggest that these terms only be used in the strong and restricted sense. Species selection, for example, should connote an irreducibility to individual organisms (because populations are acting as units of selection); it should not merely offer a convenient alternative description for

the effects of traditional selection upon organisms.

The logic of species selection is sound, and few evolutionists would now doubt that it can occur in principle. The issue, again and as always in natural history, is one of relative frequency; how often does species selection occur, and how important is it in the panoply of evolutionary events. Fisher himself dismissed species selection because, relative to organisms, species are so few in number (within a clade) and so long in duration (48):

The relative unimportance of this as an evolutionary factor would seem to follow decisively from the small number of closely related species which in fact do come into competition, as compared to the number of individuals in the same species; and from the vastly greater duration of the species compared to the individual.

But Fisher's argument rests on two hidden and questionable assumptions. (i) Mass selection can almost always be effective in transforming entire populations substantially in phenotype. The sheer number of organisms participating in this efficient process would then swamp any effect of selection among species. But if stasis be prevalent within established species, as the theory of punctuated equilibrium asserts and as paleontological experience affirms (overwhelmingly for marine invertebrates, at least), then the mere existence of billions of individuals and millions of generations guarantees no substantial role for directional selection upon organisms. (ii) Species selection depends on direct competition among species. Fisher argues for differential death (extinction) as the mechanism of species selection. I suspect, however, that differential frequency of speciation (selection by birth) is a far more common and effective mode of species selection. It may occur without direct competition between species, and can rapidly shift the average phenotype within a clade in regimes of random extinction.

J. Maynard Smith (49) has raised another objection against species selection: simply, that most features of organisms represent "things individual creatures do." How, he asks, could one attribute the secondary palate of mammals to species selection? But the origin of a feature is one thing (and I would not dispute traditional selection among organisms as the probable mechanism for evolving a secondary palate), and the spread of features through larger clades is another. Macroevolution is fundamentally about the combination of features and their differential spread. These phenomena lie

comfortably within the domain of effective species selection. Many features must come to prominence primarily through their fortuitous phyletic link with high speciation rates. Mammals represent a lineage of therapsids that may have survived (while all others died) as a result of small body sizes and nocturnal habits. Was the secondary palate a key to their success, or did it piggyback on the high speciation rates often noted (for other reasons) in small-bodied forms. Did mammals survive the Cretaceous extinction, thereby inheriting the world from dinosaurs, as a result of their secondary palate, or did their small size again preserve them during an event that differentially wiped out large creatures.

Evolutionary Pattern by Interaction Between Levels

The hierarchical model, with its assertion that selection works simultaneously and differently upon individuals at a variety of levels, suggests a revised interpretation for many phenomena that have puzzled people where they implicitly assumed causation by selection upon organisms. In particular, it suggests that negative interaction between levels might be an important principle in maintaining stability or holding rates of change within reasonable bounds.

The "selfish DNA" hypothesis, for example, proposes that much middle-repetitive DNA exists within genomes not because it provides Darwinian benefits to phenotypes, but because genes can (in certain circumstances) act as units of selection. Genes that can duplicate themselves and move among chromosomes will therefore accumulate copies of themselves for their own Darwinian reasons. But why does the process ever stop? The authors of the hypothesis (45) suggest that phenotypes will eventually "notice" the redundant copies when the energetic cost of producing them becomes high enough to entail negative selection at the level of organisms. Stability may represent a balance between positive selection at the gene level and the negative selection it eventually elicits at the organism level.

All evolutionary textbooks grant a paragraph or two to a phenomenon called "overspecialization," usually dismissing it as a peculiar and peripheral phenomenon. It records the irony that many creatures, by evolving highly complex and ecologically constraining features for their immediate Darwinian advantage, virtually guarantee the short duration of their species by restricting its

capacity for subsequent adaptation. Will a peacock or an Irish elk survive when the environment alters radically? Yet fancy tails and big antlers do lead to more copulations in the short run of a lifetime. Overspecialization is, I believe, a central evolutionary phenomenon that has failed to gain the attention it deserves because we have lacked a vocabulary to express what is really happening: the negative interaction of species-level disadvantage and individual-level advantage. How else can morphological specialization be kept within bounds, leaving a place for drab and persistent creatures of the world. The general phenomenon must also regulate much of human society, with many higher-level institutions compromised or destroyed by the legitimate demands of individuals (high salaries of baseball stars, perhaps).

Some features may be enhanced by positive interaction between levels. Stenotopy in marine invertebrates, for example, seems to offer advantages at both the individual level (when environments are stable) and at the species level (boosting rates of speciation by brooding larvae and enhancing possibilities for isolation relative to eurytopic species with planktonic larvae). Why then do eurytopic species still inhabit our oceans? Suppression probably occurs at the still higher level of clades, by the differential removal of stenotopic branches in major environmental upheavals that accompany frequent mass extinctions in the geological record.

If no negative effect from a higher level suppressed an advantageous lower-level phenomenon, then it might sweep through life. Sex in eukaryotic organisms may owe its prominence to unsuppressed positive interaction between levels. The advantages of sex have inspired a major debate among evolutionists during the past decade. Most authors seek traditional explanation in terms of benefit to organisms (50), for example, better chance for survival of some offspring if all are not Xeroxed copies of an asexual parent, but the genetically variable products of two individuals. Some, however, propose a spread by species selection, for example, by vastly higher speciation rates in sexual creatures (51).

The debate has often proceeded by mutual dismissal, each side proclaiming its own answers correct. Perhaps both are right, and sex predominates because two levels interact positively and are not suppressed at any higher level. No statement is usually more dull and unenlightening than the mediator's claim, "you're both right." In this case, however, we must adopt a different view of biological

organization itself to grasp the mediator's wisdom—and the old solution, for once, becomes interesting in its larger implication. We live in a world with reductionist traditions, and do not react comfortably to notions of hierarchy. Hierarchical theories permit us to retain the value of traditional ideas, while adding substantially to them. They traffic in accretion, not substitution. If we abandoned the “either-or” mentality that has characterized arguments about units of selection, we would not only reduce fruitless and often acrimonious debate, but we would also gain a deeper understanding of nature's complexity through the concept of hierarchy.

A Higher Darwinism?

What would a fully elaborated, hierarchically based evolutionary theory be called? It would neither be Darwinism, as usually understood, nor a smoothly continuous extension of Darwinism, for it violates directly the fundamental reductionist tradition embodied in Darwin's focus on organisms as units of selection.

Still, the hierarchical model does propose that selection operates on appropriate individuals at each level. Should the term “natural selection” be extended to all levels above and below organisms; there is certainly nothing unnatural about species selection. Some authors have extended the term (48), while others, Slatkin for example (52), restrict natural selection to its usual focus upon individual organisms: “Species selection is analogous to natural selection acting on an asexual population” (52).

Terminological issues aside, the hierarchically based theory would not be Darwinism as traditionally conceived; it would be both a richer and a different theory. But it would embody, in abstract form, the essence of Darwin's argument expanded to work at each level. Each level generates variation among its individuals; evolution occurs at each level by a sorting out among individuals, with differential success of some and their progeny. The hierarchical theory would therefore represent a kind of “higher Darwinism,” with the substance of a claim for reduction to organisms lost, but the domain of the abstract “selectionist” style of argument extended.

Moreover, selection will work differently on the objects of diverse levels. The phenomena of one level have analogs on others, but not identical operation. For example, we usually deny the

effectiveness of mutation pressure at the level of organisms. Populations contain so many individuals that small biases in mutation rate can rarely establish a feature if it is under selection at all. But the analog of mutation pressure at the species level, directed speciation (directional bias toward certain phenotypes in derived species), may be a powerful agent of evolutionary trends (as a macroevolutionary alternative to species selection). Directed speciation can be effective (where mutation pressure is not) for two reasons: first, because its effects are not so easily swamped (given the restricted number of species within a clade) by differential extinction; second, because such phenomena as ontogenetic channeling in phyletic size increase suggest that biases in the production of species may be more prevalent than biases in the genesis of mutations.

Each level must be approached on its own, and appreciated for the special emphasis it places upon common phenomena, but the selectionist style of argument regulates all levels and the Darwinian vision is extended and generalized, not defeated, even though Darwinism, strictly constructed, may be superseded. This expansion may impose a literal wisdom upon that famous last line of *Origin of Species*, “There is grandeur in this view of life.”

Darwin, at the centenary of his death, is more alive than ever. Let us continue to praise famous men.

References and Notes

1. I have argued [*Nat. Hist.* 91, 16 (April 1982)] that a third and larger theme captures the profound importance and intellectual power of Darwin's work in a more comprehensive way: his successful attempt to establish principles of reasoning for historical science. Each of his so-called “minor” works (treatises on orchids, worms, climbing plants, coral reefs, barnacles, for example) exhibits both an explicit and a covert theme—and the covert theme is a principle of reasoning for the reconstruction of history. The principles can be arranged in order of decreasing availability of information, but each addresses the fundamental issue: how can history be scientific if we cannot directly observe a past process: (i) If we can observe present processes at work, then we should accumulate and extrapolate their results to render the past. Darwin's last book, on the formation of vegetable mold by earthworms (1881), is also a treatise on this aspect of uniformitarianism. (ii) If rates are too slow or scales too broad for direct observation, then try to render the range of present results as stages of a single historical process. Darwin's first book on a specific subject, the subsidence theory of coral atolls (1842), is (in its covert theme) a disquisition on this principle. (iii) When single objects must be analyzed, search for imperfections that record constraints of inheritance. Darwin's orchid book (1862), explicitly about fertilization by insects, argues that orchids are jury-rigged, rather than well built from scratch, because structures that attract insects and stick pollen to them had to be built from ordinary parts of ancestral flowers. Darwin used all three principles to establish evolution as well: (i) observed rates of change in artificial selection, (ii) stages in the process of speciation displayed by modern populations, and (iii) analysis of vestigial structures in various organisms. Thus, we should not claim that all Darwin's
- books are about evolution. Rather, they are all about the methodology of historical science. The establishment of evolution represents the greatest triumph of the method.
2. C. Darwin, *The Descent of Man* (Murray, London, ed. 2, 1889), p. 61.
3. G. J. Romanes, *Darwin, and After Darwin* (Longmans, Green, London, 1900), pp. 1–36.
4. Failure to recognize that all creationists accepted selection in this negative role led Eiseley to conclude falsely that Darwin had “borrowed” the principle of natural selection from his predecessor E. Blyth [L. Eiseley, *Darwin and the Mysterious Mr. X* (Dutton, New York, 1979)]. The Reverend William Paley's classic work *Natural Theology*, published in 1803, also contains many references to selective elimination.
5. By “random” in this context, evolutionists mean only that variation is not inherently directed towards adaptation, not that all mutational changes are equally likely. The word is unfortunate, but the historical tradition too deep to avoid.
6. E. D. Cope, *The Origin of the Fittest* (Appleton, New York, 1887).
7. L. G. Wilson, Ed., *Sir Charles Lyell's Scientific Journals on the Species Question* (Yale Univ. Press, New Haven, Conn., 1970), p. 369.
8. Darwin was convinced, for example, in part by reading a theological work arguing that extreme rapidity (as in the initial spread of Christianity) indicated a divine hand, that gradual and continuous change was the mark of a natural process [H. Gruber, *Darwin on Man* (Dutton, New York, 1974)].
9. C. Darwin, *The Structure and Distribution of Coral Reefs* (Smith, Elder, London, 1842).
10. ———, *The Formation of Vegetable Mould, Through the Action of Worms* (Murray, London, 1881).
11. The following works have done great service in identifying and correcting this confusion: G. C. Williams, *Adaptation and Natural Selection* (Princeton Univ. Press, Princeton, N.J., 1966); J. Maynard Smith, *The Evolution of Sex* (Cambridge Univ. Press, New York, 1978).
12. A persuasive case for Darwin's active interest in this subject and for his commitment to individual selection has been recently made by M. Ruse, *Ann. Sci.* 37, 615 (1980).
13. C. Darwin, *On the Origin of Species* (Murray, London, 1859).
14. S. S. Schweber, *J. Hist. Biol.* 10, 229 (1977).
15. S. Tax, Ed., *Evolution After Darwin* (Univ. of Chicago Press, Chicago, 1960), vols. 1–3.
16. J. Huxley, *Evolution, the Modern Synthesis* (Allen & Unwin, London, 1942).
17. For example: “The opposing factions became reconciled as the younger branches of biology achieved a synthesis with each other and with the classical disciplines; and the reconciliation converged upon a Darwinian center” (16, p. 25).
18. E. Mayr, *Systematics and the Origin of Species* (Columbia Univ. Press, New York, 1942); G. G. Simpson, *Tempo and Mode in Evolution* (Columbia Univ. Press, New York, 1944); B. Rensch, *Neuere Probleme der Abstammungslehre* (Enke, Stuttgart, 1947); G. L. Stebbins, *Variation and Evolution in Plants* (Columbia Univ. Press, New York, 1950).
19. S. J. Gould, in *The Evolutionary Synthesis*, E. Mayr and W. B. Provine, Eds. (Harvard Univ. Press, Cambridge, Mass., 1980), p. 153.
20. S. J. Gould, *Dobzhansky and the Modern Synthesis*, introduction to reprint of first (1937) edition of Th. Dobzhansky, *Genetics and the Origin of Species* (Columbia Univ. Press, New York, 1982).
21. D. Lack, *Darwin's Finches* (Harper Torchbook Edition, New York, 1960).
22. This statement appears as the first paragraph in the preface to (21).
23. E. Mayr, in *The Evolutionary Synthesis*, E. Mayr and W. B. Provine, Eds. (Harvard Univ. Press, Cambridge, Mass., 1980), p. 1.
24. S. Orzack, *Paleobiology* 7, 128 (1981).
25. M. J. D. White, *ibid.*, p. 287.
26. G. L. Stebbins and F. J. Ayala, *Science* 213, 967 (1981).
27. J. L. King and T. H. Jukes, *ibid.* 164, 788 (1969).
28. S. J. Gould, *Paleobiology* 6, 119 (1980).
29. C. Darwin (13, p. 189). On the day before publication of the *Origin of Species*, T. H. Huxley wrote to Darwin (letter of 23 November 1859): “You load yourself with an unnecessary difficulty in adopting *Natura non facit saltum* so unreservedly.”
30. S. J. Gould, *The Uses of Heresy*, introduction to the republication of the 1940 edition of R. Goldschmidt, *The Material Basis of Evolution* (Yale Univ. Press, New Haven, Conn., 1982).

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