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## Tempo and mode in the macroevolutionary reconstruction of Darwinism

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**ABSTRACT** Among the several central meanings of Darwinism, his version of Lyellian uniformitarianism—the extrapolationist commitment to viewing causes of small-scale, observable change in modern populations as the complete source, by smooth extension through geological time, of all magnitudes and sequences in evolution—has most contributed to the causal hegemony of microevolution and the assumption that paleontology can document the contingent history of life but cannot act as a domain of novel evolutionary theory. G. G. Simpson tried to combat this view of paleontology as theoretically inert in his classic work, *Tempo and Mode in Evolution* (1944), with a brilliant argument that the two subjects of his title fall into a unique paleontological domain and that modes (processes and causes) can be inferred from the quantitative study of tempos (pattern). Nonetheless, Simpson did not cash out his insight to paleontology’s theoretical benefit because he followed the strict doctrine of the Modern Synthesis. He studied his domain of potential theory and concluded that no actual theory could be found—and that a full account of causes could therefore be located in the microevolutionary realm after all. I argue that Simpson was unduly pessimistic and that modernism’s belief in reductionistic unification (the conventional view of Western intellectuals from the 1920s to the 1950s) needs to be supplanted by a postmodernist commitment to pluralism and multiple levels of causation. Macro- and microevolution should not be viewed as opposed, but as truly complementary. I describe the two major domains where a helpful macroevolutionary theory may be sought—unsmooth causal boundaries between levels (as illustrated by punctuated equilibrium and mass extinction) and hierarchical expansion of the theory of natural selection to levels both below (gene and cell-line) and above organisms (demes, species, and clades). Problems remain in operationally defining selection at non-organismic levels (emergent traits vs. emergent fitness approaches, for example) and in specifying the nature and basis of levels, but this subject should be the central focus in formulating a more ample and satisfactory general theory of evolution on extended Darwinian principles.

### Darwin’s Uniformitarianism and the Downgrading of Macroevolution

We yearn to capture the essence of complexity in a line. Rabbi Hillel (ca. 30 B.C.–A.D. 10) wrote: “What is hateful to you do not do to your neighbor. That is the whole Torah. The rest is commentary.” And Marcus Aurelius, a century later and a culture apart, stated: “Look to the essence of a thing, whether it be a point of doctrine, of practice, or of interpretation.”

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But conceptual complexity is not reducible to a formula or epigram (as we taxonomists of life’s diversity should know better than most). Too much ink has been wasted in vain attempts to define the essence of Darwin’s ideas, or Darwinism itself. Mayr (1) has correctly emphasized that many different, if related, Darwinisms exist, both in the thought of the eponym himself, and in the subsequent history of evolutionary biology—ranging from natural selection, to genealogical connection of all living beings, to gradualism of change.

It would therefore be fatuous to claim that any one legitimate “essence” can be more basic or important than another. Yet I wish to focus on a Darwinism that is more pervasive than some of the other meanings—a status won by its role as the fundamental operational, or methodological postulate of all Darwin’s theorizing and experimentation.

Charles Lyell was Darwin’s guru and intellectual father figure. Darwin commented, in a statement that (for once in his writing) does not reek of false modesty in proper Victorian taste, “I always feel as if my books came half out of Lyell’s brain” (2). Much of Lyell’s thinking did not contribute to Darwin’s evolutionism and may have acted as an impediment to transmutation—in particular, Lyell’s steady-state vision of change without direction. But we can scarcely doubt that Lyell’s major working postulate and philosophical premise—his uniformitarian vision—became just as firmly embedded in Darwin’s thought and scientific action.

Lyell’s uniformitarianism held that the full panoply of past events, even those of greatest extent and apparent effect, must be explained as extrapolations from causes now operating at their current observable rates and intensities. In other words, and invariably, the small and immediate may be extended and smoothly accumulated—drop by drop and grain by grain—through time’s immensity to produce all scales of historical events. Time is the great enabler. No uniquenesses should be attributed to events of large scale and long times; no principles need be established for the great and the lengthy; all causality resides in the smallness of the observable present, and all magnitudes may be explained by extrapolation.

Darwin accepted and promulgated Lyell’s uniformitarian vision in all its uncompromising intensity. Extrapolationism (the methodological side of uniformity) underlies and unites the otherwise disparate pieces and opinions in the *Origin of Species*. What other principle could coordinate, for example, Darwin’s hostility to mass extinction (ref. 3, pp. 317–329), his brilliant section on graded structural transition in the evolution of complex and “perfect” organs like the eye (ref. 3, pp. 186–189), his initial case of pigeon breeding as a model for change at all scales (ref. 3, pp. 20–28), and even his choice of the phrase “natural selection” as an analogy to small-scale changes produced by breeders and called “artificial selection.”

Consider just two statements from the *Origin of Species* on the power of geological time to build small and present changes into any observed or desired effect. First, on nature's greater power based on time and fuller scrutiny:

As man can produce and certainly has produced a great result by his methodical and unconscious means of selection, what may not nature effect? Man can act only on external and visible characters: nature cares nothing for appearances. . . She can act on every internal organ, on every shade of constitutional difference, on the whole machinery of life. . . How fleeting are the wishes and efforts of man! how short his time! and consequently how poor will his products be, compared with those accumulated by nature during whole geological periods. (ref. 3, p. 83)

Second, on time's promotion of the infinitesimal to great magnitude:

It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages. (ref. 3, p. 84)

The pure extrapolationism of Darwin's uniformitarian perspective creates an enormous, if not fatal, problem for paleontology. We would like to be a source of meaningful evolutionary theory, for this discipline explains the patterning of the objects we study. But if every event at our scale may be built by extrapolation from a present that contains all causes, then we have no theoretical contribution to make. We are still needed in a lesser role, of course, for history is massively contingent, as Darwin well knew, and theory must therefore underdetermine actual events. But paleontology, in this status, only provides phenomenology—a descriptive accounting, dedicated to documenting that life followed this particular pathway, rather than another route equally plausible in theory. Moreover, paleontology, in Darwin's view, cannot even provide particularly good phenomenology (however honored *faute de mieux*) because an imperfect fossil record so blots, confuses, and distorts the pathway. Remember that Darwin's first geological chapter bears no triumphant title, but rather the apologetic: "On the Imperfection of the Geological Record."

The demotion imposed by pure extrapolationism—to description devoid of theory—must be the chief source of paleontology's curiously low and almost ironic reputation: to be beloved and glamorized by the public (with a series of images from *Indiana Jones* to *Jurassic Park*), and almost invisible within professional halls of status and funding. Consider two assessments of our absent contribution to evolutionary theory. Sadly, as Julian Huxley notes in beginning the first quote, paleontologists have often defended their own debasement—an all too common phenomenon noted among slaves, hostages, and other oppressed people who adopt the assessments of their captors (psychologists even have a label for it, as the Patty Hearst syndrome). Huxley wrote in the book that gave our theory its name (ref. 4, p. 38):

As admitted by various paleontologists, a study of the course of evolution cannot be decisive in regard to the method of evolution. All that paleontology can do in this latter field is to assert that, as regards the type of organisms which it studies, the evolutionary methods suggested by the geneticists and evolutionists shall not contradict its data.

And even so iconoclastic a morphologist as D. Dwight Davis stated for the Princeton meeting on genetics, paleontology, and evolution (ref. 5, p. 77)—the gathering that oversaw the foundation of our major professional society and its journal,

*Evolution:*

Paleontology supplies factual data on the actual rates of change in the skeleton and the patterns of phyletic change in the skeleton. Because of the inherent limitations of paleontological data, however, it cannot perceive the factors producing such changes. Attempts to do so merely represent a superimposition of neobiological concepts on paleontological data.

Such invalid statements in professional publications often follow an unfortunate path towards inclusion in basic textbooks—and errors in this particular medium are almost immune to natural selection, as extinction-proof as a living fossil in the deep ocean. One major, and very fine, introductory text (ref. 6, p. 524) states:

Evolution can be studied on the population level only with living organisms. The fossil record provides too few data to allow such treatment; it merely allows paleontologists to reconstruct the history of animal and plant groups [the restriction of our efforts to descriptive phenomenology]. The population approach makes it possible to ask such questions as: What is the rate of evolution in a given species? What factors influence the course or rate of evolution? What conditions are necessary for evolution to begin or cease?

Funny. I would include these three questions within a set most amenable to resolution by the data of fossils and their temporal distribution!

As a final illustration of the reductionistic biases that still beset this most comprehensive of fields, and of the usual tendency to ignore or devalue theory based on whole organisms or long times, the assigned reporter for *Science* magazine presented a remarkably skewed and parochial view of the conference that honored Simpson's *Tempo and Mode* at its half-century, and formed the basis for this published symposium (7). The meeting itself was broad and comprehensive, with talks spanning a full range of levels and durations, from molecules at moments to faunas over geological periods. Yet the reporter ignored about two-thirds of the presentations, including all from Simpson's own professional domain, and focused entirely upon molecular insights—a central issue to be sure, but surely not the exclusive or even the primary theme of a meeting called to honor Simpson's work and its sequelae. Under the headline "Will Molecular Data Set the Stage for a Synthesis," *Science*'s one-dimensional reviewer got Simpson's title wrong and then stated:

Fifty years ago, the great evolutionary biologist George Gaylord Simpson . . . published a classic volume called *Tempo and Mode of (sic) Evolution*. . . Fifty years later, 250 leading evolutionary theorists gathered in Irvine, California at a symposium in Simpson's honor. Appropriately, the aim of the symposium was to provide a Simpsonian overview of the field, and the conclusion was that its tempo of change is rapid, and one of the main modes of change is the acquisition of new data from molecular biology. As one presentation after another confirmed, molecular biology is offering researchers a multitude of new genetic clues about evolutionary change.

A picture of Simpson, smiling benignly (as he did only rarely in life), graces the page. But I can guarantee *Science*'s reporter that Simpson's ghost is raging at the exclusion of his own field from the primary account of his splendid party.

#### Tempo and Mode: A Potential Solution Undermined

The conventional view of the Modern Synthetic theory of evolution (often called or equated with Neo-Darwinism) envisages two sequential stages of development: formulation of the population-genetic core in the 1920s and 1930s through the work of R. A. Fisher, Sewall Wright, and J. B. S. Haldane; and alignment of more traditional disciplines in

natural history with this central theory in a series of books beginning with Dobzhansky in 1937 (8), and continuing with Mayr in 1942 for systematics (9), Simpson in 1944 for paleontology (10), and Stebbins in 1950 for botany (11), among several others. Simpson's *Tempo and Mode in Evolution*,\* published 50 years ago, is our century's most important book in paleontological theory, and my profession's chief contribution to the evolutionary sciences.

Simpson wrote *Tempo and Mode* to assert a distinctive theoretical corner for paleontology in evolutionary discussion and to counteract the denigration discussed in the first section of this paper. (That he was not entirely successful will be evident from the fact that most of the deprecatory quotations, cited earlier in this article, postdate the publication of his book. I shall argue, in this section, that Simpson failed because he bowed to the wrong solution in claiming that he could locate nothing distinctive after correctly defining a domain where one might look.) He spoke for paleontology, and against the extrapolationist vision, with some bravado in his introduction (ref. 10, p. xvii):

They [geneticists] may reveal what happens to a hundred rats in the course of ten years under fixed and simple conditions, but not what happened to a billion rats in the course of ten million years under the fluctuating conditions of earth history. Obviously, the latter problem is much more important.

*Tempo and Mode*, like so many seminal books, lies completely outside the traditions of its profession. To be sure, paleontologists had written copiously about "evolution;" but, in the profession, this word referred to the documentation of history, specifically to the establishment of phylogeny, not to a study of processes and mechanisms. Paleontological works on evolution proceeded in descriptive and chronological order. If they attempted any closing statements on theoretical generalities, they tried to portray such conclusions as inductions in the enumerative mode from the facts of phylogeny—hence, the various "laws"—Cope's, Williston's, Dollo's—of the classical literature. Simpson turned this procedure around. Instead of an exhaustive tome in documentation, he wrote 217 pages of stimulating suggestions. He started from the principles of neontological Darwinism as he saw the theory emerging. He then asked if major features of the fossil record could be reconciled to this modern version of Darwinism, without postulating any special macroevolutionary theory. *Tempo and Mode* contains 36 figures, but only one portrays an animal—actually only the lower second molar and fourth premolar of the Eocene condylarth *Phenacodus*, cribbed from Osborn (ref. 10, figure 9, p. 43). The rest are graphs, frequency distributions, and pictorial models. No paleontological innovation could have been more stunning than this.

But the most innovative feature of all resides in Simpson's well-chosen title, for he properly selected tempo and mode as the two paleontological subjects that might provide novel theory, and not just phenomenology, to the evolutionary sciences. His title is, therefore, a statement about paleontological relevance, a defense of the theoretical importance of those ten billion rats.

There is much, of course, that paleontology cannot do—based on imperfection of the record, and our imposed inability to observe or manipulate past processes directly. But, in specifying tempo and mode, Simpson sought to isolate and

feature the theoretically tractable subjects of paleontology. His argument is both simple and elegant: paleontology has unique access to questions of evolutionary tempo, which require the direct data of long durations. These paleontological tempos can and should be quantified to attain a testable generality transcending the "feel" and expertise of taxonomic specialists on given groups.† Rigorous and quantitative studies of tempo (or pattern) can lead to inferences about modes (or processes). Scientific theory is, essentially, the attempt to explain nature's processes. By using uniquely paleontological data about pattern to infer the unseeable processes of long temporal spans, paleontology may be an active purveyor of evolutionary theory.

This strategy of using uniquely paleontological data about tempo to infer mode, and thus to develop theory directly from the domain of macroevolution, pervades Simpson's book and underlies all his examples. To cite just two cases:

(i) Designation of the three modes. Simpson's last, and best-known, chapter (ref. 10, pp. 197–217) uses data of tempo to propose a fundamental division of evolutionary processes into three modes, each with different meaning: *speciation* for a low-level process of iterating diversity, with no significant input to trends or other larger-scale patterns; *phyletic evolution* for the ordinary style of directional change, leading to evolutionary trends and accounting for some 90% of paleontological data; and *quantum evolution* for rapid and rare, but efficacious, "all-or-nothing" transitions from one adaptive zone to another through an inadaptable phase (a process analogized with Wright's model of genetic drift).

(ii) The theory of horotely, tachytely, and bradytely. This fascinating and brilliant, if ultimately flawed, theory has been widely misunderstood by people who do not grasp Simpson's central strategy of using tempo to infer mode. Many critics have stated that Simpson only invented some arcane, Greek-based jargon to divide the ordinary continuum of evolutionary rates into slow (brady), ordinary (horo), and fast (tachy). Not at all. Simpson was trying to identify separate peaks (modes in the statistical sense) in the distribution of tempos in order to specify distinct modes (in the ordinary sense) of evolution. Thus, horotely is not the central tendency of a single distribution of rates (with tachytely as the right tail, and bradytely as the left tail, as in the conventional misinterpretation); horotely is the *entire distribution* of ordinary rates, while tachytely and bradytely are, in Simpson's hypothesis, smaller distributions with distinct central tendencies at much larger and much smaller values than the central tendency of the horotelic distribution.

Simpson based this hypothesis upon a fascinating treatment of data on generic longevity. He contrasted extant with extinct genera by plotting longevities as conventional survivorship curves. Extinct genera fit the ecological models without anomaly, but extant genera yielded a hump of "too many" values at extended longevities—in other words, too many living bivalve genera had inhabited our planet for too long according to random models of survivorship. Simpson called this hump the bradytelic distribution. (The tachytelic

\*The *Science* reporter's error in citing the book as *Tempo and Mode of Evolution* is important, and not an insignificant difference in a meaningless preposition. Simpson was a great and careful writer, who used words with meticulous precision (and was an English major in college). He did not write his book to discourse on the tempo and mode of evolution in general, but to advance the key claim that tempo and mode are paleontology's distinctive subjects for winning insight into the causes of evolution.

†Among leaders of the second phase of the synthesis, only Simpson was well trained mathematically, and only he could read the primary source material of the first phase with full understanding. (Dobzhansky, for example, often stated that he adopted a "father knows best" approach in his collaborations with Sewall Wright—that is, he simply accepted Wright's verbal interpretation because he could not understand Wright's equations in their own joint papers!) Simpson was mathematically adept and a particularly fine statistician. His textbook, *Quantitative Zoology*, written with his wife Anne Roe, was a standard source for decades, and remains unmatched for clarity and well-chosen examples. How ironic that words built the bridge to the second phase, while formulae constructed the pillars and anchor of the first phase—so that, with Simpson's exception, the crucial linkage rested upon faith.

distribution then emerged as a theoretical concept for a spectrum of rates too rapid to be recorded in most geological circumstances, and therefore responsible for the notorious gaps of the fossil record, even in relatively complete stratigraphic sections.)

Following his usual argument, Simpson then tied each of the three distributions of tempos to distinct modes of evolution—horotely to ordinary anagenesis in phyletic evolution (responsible, he argues, for some 90% of the fossil record), tachytely to quantum evolution, and bradytely to establishment of stable forms (often called “living fossils”) in persistent adaptive zones. As a testimony to his proper restriction of science to the operational, Simpson said little about tachytely (which can rarely be measured and must be inferred from gaps in the record), basing his entire conception upon an attempt to identify and quantify the tractable bradytelic distribution through analysis of survivorship data, as described above.

Simpson’s general argument is both illuminating and correct: tempos are a unique paleontological domain; modes may be inferred from them, and status as a source for theory thus conferred upon paleontology. Why, then, did Simpson’s work fail to establish such a role for the fossil record and not lead to an independent body of macroevolutionary theory—as the deprecatory quotes cited in section one of this paper, all postdating *Tempo and Mode*, demonstrate? Two reasons can resolve this only apparent paradox:

(i) The dilemma imposed upon paleontology by the Synthesis. The second phase of the Synthesis had a central theme—to bring each traditional subdiscipline of natural history under the explanatory rubric of the first phase, by showing that all results could be rendered consistent with population genetics and Mendelian principles of microevolutionary change. Since paleontology had the oldest and deepest tradition for denying such a claim, and asserting the need for principles contrary to Darwinism in explaining evolution in the fullness of time (orthogenesis, various forms of vitalism and finalism), Simpson felt especially compelled to argue that the entire past, in all magnitude and duration, could be fully encompassed by extrapolation from microevolutionary principles of the moment—Darwinian uniformitarianism in its purest form.

Thus, although Simpson did enunciate a methodology—modes from tempos—for discovering uniquely macroevolutionary theory, he applied the procedure to deny this possible outcome. In other words, he developed a method that might have yielded theory, and then claimed that none was to be found. And this conclusion was no passive or subsidiary result of other purposes, but the central goal—and, in Simpson’s view, the intellectual triumph—of his work. Paleontology became a dutiful son to the synthesis, and no longer an unruly child. Simpson concluded, with evident satisfaction (ref. 10, p. 124):

The materials for evolution and the factors inducing and directing it are also believed to be the same at all levels and to differ in mega-evolution only in combination and in intensity. From another point of view mega-evolution is, according to this theory, only the sum of a long, continuous series of changes that can be divided taxonomically into horizontal phyletic subdivisions of any size, including subspecies.

(ii) Simpson’s later moves to greater conventionality. Of his three evolutionary modes, Simpson always emphasized the one—phyletic evolution—most supportive of extrapolationism, for trends in the phyletic mode work by pure, step-by-step anagenetic accumulation, the “march of frequency distributions” through time. He exalted the phyletic mode as primary by two strategies. First, by asserting the predominant relative frequency of this maximally extrapolationist mode—the 9/10 figure previously cited: “Nine-tenths

of the pertinent data of paleontology fall into patterns in the phyletic mode” (ref. 10, p. 203).

As a second strategy, he downplayed the other two modes. He saw speciation as a low-level process, capable only of producing iterated variety (and perhaps of protecting adaptations by sorting them into several lineages), but not as participating in sustained evolutionary trends: “This sort of differentiation draws mainly on the store of preexisting variability in the population. The group variability is parceled out among subgroups. . . . The phenotypic differences involved in this mode of evolution are likely to be of a minor sort or degree. They are mostly shifting averages of color patterns and scale counts, small changes in sizes and proportions, and analogous modifications” (ref. 10, p. 201).

But quantum evolution posed a different challenge to the dominance of phyletic extrapolationism. Simpson had never granted quantum evolution a high relative frequency, but he did regard this mode as responsible for some of the most profound anatomical transitions in life’s history. In *Tempo and Mode*, Simpson did present quantum evolution as an alternative to the phyletic mode, with different primary causes (though still tolerably uniformitarian in invoking Wright’s genetic drift). But Simpson radically changed his view in his larger, and far more conservative, later book, *The Major Features of Evolution* (12). He now demoted quantum evolution from a separate mode to merely an extreme value in the phyletic spectrum. He began by denying any efficacy to Wright’s process: “Genetic drift is certainly not involved in all or in most origins of higher categories, even of very high categories such as classes or phyla” (ref. 12, p. 355). He then redefined quantum evolution as one among four styles of phyletic evolution, all characterized by “the continuous maintenance of adaptation” (ref. 12, p. 385). Quantum evolution was therefore transmogrified from a distinct mode to extrapolative accumulation of adaptive change at fastest rates: Quantum evolution, he now claimed, “is not a different sort of evolution from phyletic evolution, or even a distinctly different element of the total phylogenetic pattern. It is a special, more or less extreme and limiting case of phyletic evolution” (ref. 12, p. 389).

I see a kind of supreme irony in Simpson’s argument and its ontogenetic development. He made a brilliant and expansive move in recognizing that paleontology had access to theory through the quantification of tempos and inference of modes. But he then found no theory where it might have resided, and he became ever more wedded to the synthetic proposition that all in time’s vastness could be rendered by extrapolation from Darwinian processes seen in the genetics of modern populations. Paleontology therefore remained the subsidiary playing field for a game with rules fully specified elsewhere. Simpson hoped to win respect for paleontology by defining his field as an ally to the synthesis but, as in politics and war, faithfulness without independence will be used to the utmost, but never really honored with equality.

### A Solution in Bonded Independence

Dichotomy is both our preferred mental mode, perhaps intrinsically so, and our worst enemy in parsing a complex and massively multivariate world (both conceptual and empirical). Simpson, in discussing “the old but still vital problem of micro-evolution as opposed to macro-evolution” (ref. 10, p. 97), correctly caught the dilemma of dichotomy by writing (ref. 10, p. 97): “If the two proved to be basically different, the innumerable studies of micro-evolution would become relatively unimportant and would have minor value for the study of evolution as a whole.”

Faced with elegant and overwhelming documentation of microevolution, and following the synthesists’s program of theoretical reduction to a core of population genetics, Simp-

son opted for denying any distinctive macroevolutionary theory and encompassing all the vastness of time by extrapolation. But if we drop the model of dichotomous polarization, then other, more fruitful, solutions become available.

The Synthesis arose in a reductionistic age, as best evidenced by the contemporary "unity of science" movement initiated by philosophers of the Vienna Circle (see ref. 13, for a fascinating account of these links), and by the general intellectual context now called modernism, and then so dominant in a variety of fields from architecture to classical music. Modernism's emphasis on the abstract, the simplified, the fully universal, the underlying principles that build the unique and complex from the small and general, all fueled the preference within evolutionary biology for a comprehensive micro-level theory that could build all scales and sizes by smooth extrapolation. Theory introduced at the macro-level seemed antithetical—a true dichotomous contrary—to such a program.

We now live in an age of self-styled "postmodern" reformation—and though this movement has engendered silliness in architecture and incomprehensibility in literature, postmodernism has also greatly benefited intellectual life by stressing themes of pluralism, multi-level causality, virtues of complexity, individuality, and, yes, even a bit of playfulness. Modernism's hegemonic idea of universal reduction to lower-level principles and causes has been replaced by respect for the legitimacy of multiple levels and perspectives and for their causal mechanisms and insights.

In this postmodern context, it should be easy to grasp a stunningly simple and utterly unprofound solution to "the old but still vital problem of microevolution. . . [and] macroevolution." (But you do need the context to see the "obvious," hence the unavailability of this solution under modernism.) I put an ellipsis in Simpson's statement to eliminate the three words that cause all the trouble—"as opposed to." Micro- and macroevolution are not opposed, but neither does one follow by extrapolation from (and therefore become intellectually subservient to) the other. The existence of genuinely independent macroevolutionary theory does not imply that "the innumerable studies of micro-evolution would become relatively unimportant." These studies are vitally important both as controlling in their own domain, and powerfully contributory to macroevolution as well. Contributory, but neither exclusive nor decisive. No dichotomy exists. There is no single pathway of reductive explanation. Our evolutionary world is a hierarchy of levels, each of legitimacy and irreducible worth. I propose no California love-fest of "I'm OK, you're OK." Genuine pluralism is tough minded and rigorous in trying to map theoretical complexity upon our hierarchical world. Empiricism adjudicates, and some levels may turn out to be unimportant in nature, though plausible in theory. But we must entertain the legitimacy of all logically coherent levels in order to find out.

In seeking an independent body of macroevolutionary theory, not construed as contrary to microevolutionary knowledge, but viewed as truly complementary in bonding to produce a more satisfying total explanation, I would focus upon two themes that share the common feature of rejecting Darwin's uniformitarian extrapolationism, not his natural selection (or other major meanings of Darwinism).

(i) Causal boundaries between levels, breaking the possibility of smooth upward extrapolation. Darwin's uniformity requires isotropy in extension, all the way from low causal to high phenomenological; nothing in the structure of causation may break the ever-growing inclusion. But if, on the other hand, important new causes arise at higher phenomenological levels of long time or great magnitude—even if most of the results be complementary to those produced by lower-level causes (though they need not be congruent, and may well be

contrary or orthogonal)—then the extrapolationist paradigm is invalid.

I believe that nature is so hierarchically ordered in a causal sense and that distinct processes emerge at a series of ascending breakpoints in time and magnitude. To mention the two themes that have been most widely discussed in paleontological literature during the past twenty years:

(a) Punctuated equilibrium and trends within clades. Trends in the anagenetic mode may be understood as pure extrapolation and accumulation by selection (or other processes) operating at sequential moments in populations. But if species tend to be stable after geologically momentary origins, as punctuated equilibrium proposes (see ref. 14 for a best case, ref. 15 for a compendium of support, and refs. 16 and 17 for opposition), then trends must be described as the differential success of certain species within a clade (as a result of greater longevity, higher propensity to speciate, or biased direction of speciation)—and the reasons for geological success of species are both intrinsically macroevolutionary, and distinct from accumulation by natural selection within a continuously evolving population. Moreover, if the characters causing differential species success are emergent properties of species themselves (18), then the reasons for macroevolutionary change by species selection within clades are formally irreducible to conventional Darwinian selection upon organisms within populations.

(b) Mass extinction and patterns of waxing and waning among clades. Darwin, as noted above, feared and rejected mass extinction [see Raup's article in this symposium (19)]—not because such coordinated dying is inconsistent with natural selection (for nothing in this form of Darwinism guarantees that organisms can adapt to environmental change of such magnitude and rapidity), but because mass extinction breaks the extrapolative causal continuum that the uniformitarian meaning of Darwinism requires. Mass extinctions are not random, but survival through them works by different rules (see ref. 20 for a general argument, ref. 21 for an intriguing example) from those that regulate success in Darwinian struggles of normal times. Darwinian accumulation through normal times cannot, therefore, encompass the history of life. If mass extinctions only accelerated, but otherwise coincided in causal direction with events of normal times (the "turning up the gain" model in my terminology—ref. 22), or if mass extinctions were only minor patterning agents, then the extrapolative Darwinism of normal times would still rule. But mass extinctions are not coincident, and they are truly massive (up to 96% species death of marine invertebrates in a well-known estimate for the largest, late Permian great dying ref. 23). They are, therefore, causal patterning agents separate from the daily Darwinism of normal times.

(ii) The hierarchical reconstruction of the theory of natural selection. Darwin's key notion, that natural selection works almost entirely upon individual organisms as primary units, arises from several aspects of his thinking—from, for example, his uniformitarianism (for organisms are the noticeable biological objects of moments), and his overthrow of Paleyan teleology. (What a delicious irony—to claim that good organic design and ecological harmony, once seen as proof of God's wise benevolence, truly arise only as the side consequence of a process with apparently opposite ethical meaning—organisms struggling for their own benefits alone, defined as individual reproductive success.) Classical Darwinism, as a single-level theory causally focused upon organisms, makes sense in traditional terms (while the attempt of Dawkins and others to reduce the level of causality even further to genes can only be called hyperdarwinism, or more of the same; see ref. 24). Williams (ref. 25, p. 6) correctly identifies conventional Darwinian methodology: "In practice, higher levels of selection are seldom invoked,



and biologists routinely predict and find that the properties of organisms are those expected if selection operates mainly on the varying capabilities of individuals."

In this context, I believe that the most portentous and far-ranging reform and expansion of Darwinism in our generation has been the growing (26–28), if so far ill-coordinated, attempt to reconstruct the theory of natural selection as a more general process, working simultaneously on biological objects at many levels of a genealogical hierarchy. The revised theory is in no way antithetical to Darwinian natural selection and should be read as an extension rather than a replacement. But the hierarchical theory has a structure very different from conventional, single-level Darwinism working on individual organisms—so the revised theory is a fascinating novelty, not a more inclusive extrapolation. After all, there is a world of difference between the claim that nature's momentarily stable objects are optima or maxima set by one canonical form of selection and the statement that such stabilities are balances among distinct levels of selection that may work coincidentally, orthogonally, or contrarily. Since most of these newly recognized levels are intrinsically macroevolutionary (species selection, clade selection, and some forms of interdemic selection), and since their ways and modes are distinct from conventional natural selection on individuals, the hierarchical theory also affirms a substantial theoretical space for macroevolution and its paleontological basis.

To be a unit of selection, biological objects must embody five basic properties: birth points, death points, sufficient stability through their existence, reproduction, and inheritance of parental traits by offspring. (The first three properties are required to individuate any named item as a distinct entity rather than an arbitrary segment of a continuum; the last two are prerequisites for agents of Darwinian selection, defined as differential reproductive success.) Organisms are the quintessential biological objects endowed with these five properties, hence their role as canonical Darwinian individuals in the basic theory.

But many other kinds of biological objects maintain these five properties, and can therefore act as causal agents of selection. The hierarchical theory is therefore explicitly causal, and not merely phenomenological. We may start with gene selection—not the false Dawkinsian version, which tries to break all higher-level processes down to this supposedly universal locus of causality, but the proper form of genes acting "for" themselves, as in the badly named phenomenon of "selfish DNA" (29, 30). (In the general theory of selection, all objects work for themselves by struggling for differential reproductive success at their own level; multiply replicating DNA, producing no benefits to organisms thereby, can only be viewed as selfish if all evolutionary change be judged by impact upon organisms—the very Darwinian parochialism now superseded by the hierarchical theory!)

Moving up a level, Buss (31) has made a fascinating case for a distinct form of cell-lineage selection, with cancer as one mark of its pyrrhic victory over conventional selection on organisms. We next encounter ordinary Darwinian selection on organisms, a powerful mode surely responsible for adaptive design of bodies [but not, therefore, *pace* Dawkins (32), more intrinsic or more important than other evolutionary phenomena, like waxing and waning dominance among clades through geological time—a phenomenon that surely cannot be fully rendered by differential merits of adaptive design among organisms].

Moving to levels above organisms, we first encounter the confusing field of selection among groups or demes within species—a theme once infused with woolly thinking (ref. 33, for historically needed correction) that gave the entire subject a bad name, but now being treated more rigorously and surely containing much of enormous value in various modes termed interdemic, trait-group, etc. (34, 35). Above this complex

field, we encounter the two clear levels of truly macroevolutionary selection, largely based upon paleontological data, and capable of producing important phenomena of evolutionary pattern not fully rendered by causes at lower levels—species selection (36–38) for trends within clades and clade selection (25) for differential waxing and waning of monophyletic groups.

The developing field of hierarchical selection theory is beset with conceptual difficulties so thorny that I sometime wonder if our innately dichotomizing minds are sufficiently well constructed for thinking about simultaneous levels interacting in all possible modes (or perhaps I'm just stupid, although the issues seem to beset others as well). Two problems have been paramount in the developing discussion.

(i) How shall selection itself be identified and defined? Since we desire an explanatory theory, we must clearly distinguish (18) the causal process of selection (differential survival based on active and intrinsic properties of the biological objects under review), from the descriptive phenomenon of sorting (differential survival that might be causally based upon selection at lower or higher levels, yielding sorting as an effect). Even with this proviso, several partly contradictory criteria for the definition of selection as a causal process at higher levels have been proposed. Most firm and unambiguous, but most elusive and hard to document, is the "emergent trait" approach (18, 37), where selection is only identified if explicit features responsible for sorting can be specified as emergent in the objects being sorted. Differential success based on emergent traits is surely selection by anyone's definition and permits us to speak of genuine adaptation at higher levels—but emergent traits may be rare, and are surely hard to define, often demanding narrative knowledge of selective processes not available from data of fossils.

The "emergent fitness" approach (39) is more general and operational (through use of ANOVA-type models applicable to quantitative data of fossils), but fitnesses are not traits, and the analog to adaptation is thereby lost, along with clear correspondence to vernacular notions of "advantageous." This approach does, however, provide the enormous advantage of including selection upon variability as a legitimate form of causality at higher levels.

Williams (25) has proposed an even more inclusive definition for clade selection, an interesting position for a man who formerly criticized all proposed forms of group selection so brilliantly, and who became identified thereby as a champion of lower-level selection (33). Williams seems to define as higher-level selection any form of sorting between groups that can be described as nonconcordant with any simultaneously observed mode of sorting at the organism level (see his interesting hypothetical example in ref. 25, pp. 50–52).

(ii) How shall the items and units of selection be identified and defined? Two major contributors to this debate on hierarchical selection—Eldredge (40) and Williams (25)—have tried to establish parallel hierarchies of equal causal import: genealogical and ecological for Eldredge, material and codical for Williams. I believe that these efforts are ill-advised and that only the genealogical and material sequences should be viewed as causal units participating in Darwinian selection.

Williams makes his distinction between entities and information, speaking (ref. 25, p. 10) of "two mutually exclusive domains of selection, one that deals with material entities and another that deals with information and might be termed the codical domain." But I do not think that the codical domain has meaning or existence as a locus for causal units of selection, for two reasons:

(a) Odd mapping upon legitimate intuitions. Williams uses a criterion of selection that arises from an important literature developed by Hull (41), Sober (42), and others on replicators

and interactors—and that requires relatively faithful replication across generations in order to qualify an entity as a unit of selection. (Sexual organisms, dispersed and degraded by half in each offspring of the next generation, do not qualify on this criterion—a major argument advanced by gene selectionists for locating causality instead at the lower level of faithfully replicating sequences of DNA.) Williams accepts this criterion for his codical domain, thus leading to the following peculiar position: *genes* are units of selection (as the replicating consequence in the codical domain of selection upon organisms in the material domain); *gene pools* are also units of selection (as replicating consequences of higher-level selection upon groups to clades); whereas *genotypes*, in an intermediate category, are *not* units of selection (except in asexual organisms, where replication is faithful). Thus the codical domain skips a space in the hierarchy, and contains no organismic level of selection (except for asexual forms) because the corresponding codex is impersistent.

This linkage of selective agency to faithful replication has been so often repeated in the past decade that the statement has almost achieved status as dogma in evolutionary theory. Yet I think that this criterion is entirely wrong. Selection isn't about unitary persistence—never was, and never should have been so formulated. Selection is about concentration—that is, the differential passage of more of “youness” into the next generation, an increase in relative representation of the heritable part of whatever you are (whether you pass yourself on as a whole, or in disaggregated form into the future of your lineage). Consider the standard 19th Century metaphor for selection: a sieve. The sieve is shaken, and particles of a certain size become concentrated, as others pass through the net (lost by selection). Integral “you” may be disaggregated in this process, but so long as the next generation contains a relative increase in your particles, and so long as you qualified as an active causal agent of the Darwinian struggle while you lived, then you are a unit of selection (and a winning unit in this case).

(b) The codical domain as bookkeeping only. We may indeed, and legitimately as a practical measure, choose to keep track of an organism's success in selection by counting the relative representation of its genes in future generations (because the organism does not replicate faithfully and therefore cannot be traced as a discrete entity). But this practical decision for counting does not deprive the organism of status as a causal agent, nor does it grant causality to the objects counted.

The listing of accounts is bookkeeping—a vitally important subject in evolutionary biology, but not a form of causality. I think that Williams's codical domain is not an alternative realm of causality, as he claims, but just a fancy name for the necessary bookkeeping function of evolutionary calculation. Williams almost seems to admit as much in two passages (ref. 25, pp. 13 and 38):

For natural selection to occur and be a factor in evolution, replicators must manifest themselves in interactors, the concrete realities that confront a biologist. The truth and usefulness of a biological theory must be evaluated on the basis of its success in explaining and predicting material phenomena. It is equally true that replicators (codices) are a concept of great interest and usefulness and must be considered with great care for any formal theory of evolution. (ref. 25, p. 13)

Fine. But codices are units of information useful in bookkeeping, not material entities “out there” in the Darwinian struggle—and bookkeeping is not causality.

However we ultimately define the levels in a genealogical hierarchy of effective selection upon each, and however we decide to codify the criteria for identifying selection at these levels, the hierarchical, multi-level theory of natural selection should put an end to an unhappy and unhelpful conflict rooted

in the false mental tactic of dichotomization: the modes of macro- and microevolution as intrinsically opposed and in battle for a common turf. This model led the Synthesis to deny any theoretical status to macroevolution at all—thus preserving hegemony for a microevolutionary theory that could supposedly encompass all scales by smooth extrapolation. But macroevolution is complementary, not oppositional—and each domain holds unique turf (while maintaining a rich and fascinating interaction with all other realms). A grant of independence and theoretical space to a previously rejected domain does not mark a retreat or a submission, but rather a commitment to probe all the richness of nature with all the mental equipment that our limited faculties can muster. For a fine poet once stated this “Happy Thought” in *A Child's Garden of Verses*:

The world is so full of a number of things,  
I'm sure we should all be as happy as kings (43).

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