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## The paradox of the first tier: an agenda for paleobiology

Stephen Jay Gould

*Abstract.*—Nature's discontinuities occur both in the hierarchical structuring of genealogical individuals and in the distinct processes operating at different scales of time, here called tiers. Conventional evolutionary theory denies this structuring and attempts to render the larger scales as simple extrapolation from (or reduction to) the familiar and immediate—the struggle among organisms at ecological moments (conventional individuals at the first tier). I propose that we consider distinct processes at three separable tiers of time: ecological moments, normal geological time (trends during millions of years), and periodic mass extinctions.

I designate as “the paradox of the first tier” our failure to find progress in life's history, when conventional theory (first tier processes acting on organisms) expects it as a consequence of competition under Darwin's metaphor of the wedge. I suggest a resolution of the paradox: whatever accumulates at the first tier is sufficiently reversed, undone, or overridden by processes of the higher tiers. In particular, punctuated equilibrium at the second tier produces trends for suites of reasons unrelated to the adaptive benefits of organisms (conventional progress). Mass extinction at the third tier, a recurring process now recognized as more frequent, more rapid, more intense, and more different than we had imagined, works by different rules and may undo whatever the lower tiers had accumulated.

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### I. Tiers of Time

In the glory days of Victoria's reign, when a pound bought more than five American dollars, the English economy operated on two distinct tiers. The working man, paid weekly for his labor and without benefit of banking or hope of accumulation, might pass his entire life without ever seeing a pound note, for he received his wage in shillings and pence and its total never reached a full pound. Meanwhile, bankers in the City of London transacted the world's imperial business in pounds. India today operates on two similar and largely noninteracting tiers—the 100-rupee notes (about ten dollars) of the hotel shops and the bustling economy of the bazaars, where 10 rupees buys at least one of anything and no one ever sees (or could cash) a 100-rupee note.

Our world of times and amounts is not always continuous. Its metrics usually extend smoothly from one end to the other (shillings did grade to pounds and rupees are rupees), but its activities are often sharply concentrated in definite regions of a potential spectrum, with large open spaces between. Systems often drive in opposite directions away from break points; location on one or another side of a threshold inevitably

pushes toward an equilibrium far above or below.

In studying nature's discontinuities, I have been primarily interested in hierarchies—particularly the genealogical hierarchy of gene, organism, deme, species, and clade (Arnold and Fristrup 1982; Gould 1982a, b; Vrba and Eldredge 1984)—and how the discreteness of different levels imposes a punctuational style of change by establishing limited domains of stability in a broad potential field. Hierarchies are relationships of ascending inclusion. But the world is also discontinuously structured in other ways—particularly in clustering of stable points along spectra of times and amounts. I propose that we should view evolutionary time as such a system of distinct tiers—and that the problem of trans-specific evolution requires an explicit study of their interaction. Darwinian tradition leads us to deny this kind of structuring, to view time as continuous, and to seek the source of causality at all scales in observable events and processes at the smallest.

The first tier includes evolutionary events of the ecological moment. The second encompasses the evolutionary trends within lineages and clades that occur during millions of years in “normal”

geological time between events of mass extinction. In Darwinian theory, no causal differences separate these phenomena, only a quantitative increment in time and effect. But if trends occur primarily within a pattern of punctuated equilibrium, and if the differential success of species that must power such trends arises from truly emergent, species-level selection (or any other process working irreducibly at the level of species), then the Darwinian model of macroevolution as extrapolated selection among organisms must fail and trends have legitimate autonomy at the second tier. This, not any statement about rate or misunderstanding about macroevolution (Halstead 1984; Turner 1984; and other distortions so obtuse that I can only regard them as willful), is the radical content of punctuated equilibrium (see critiques of Stebbins and Ayala [1981] and Levinton [1983] for other commentaries that miss this central point and focus on peripheral or uncontroversial issues).

The most exciting subject in paleobiology today, and the source (I suspect) of its principal agenda for the 1980s, lies in our recent recognition that one of our best-recognized and most puzzling phenomena, mass extinction, is not merely more and quicker of the same, but a third distinct tier with rules and principles of its own.

The dilemma of the modern synthesis for paleobiology lay in its claim that all theory could be extrapolated from the first tier, thus converting macroevolution from a source of theory to a simple phenomenology—a body of information to document and to render consistent with a theoretical edifice derived elsewhere. But if the tiers of life create pattern by emergent rules not predictable from processes and activities at lower tiers, then paleobiology adds its special insights without contradicting principles for lower tiers.

Much of the acrimonious debate on this subject reflects a misunderstanding that claims for uniqueness at higher levels either contradict or nullify the hard-won principles of Darwinian moments. Emergent principles are additions to, not denials of, the well-established theories of microevolution. When King and Jukes (1969) called neutralism “non-Darwinian evolution,” they meant just that and no more—not “anti-Darwinian” evolution, but that something new

had been added to the legitimate corpus of Darwinian mechanisms. Similarly, if mass extinction is really driven by a regular cycle of cometary impact, and if it restructures the biosphere either randomly or by rules different from those operating in normal times, then principles for the first tier will not explain the shifting taxonomic structure of life’s diversity. (We will all, I trust, at least allow that creatures cannot prepare for catastrophes of such spacing and that their adaptive struggles at the first tier can therefore, at the very best, only produce exaptations for later debacles.)

## II. The Paradox of the First Tier

Stepping way back and looking at too broad a scale, one might discern some sort of progress in life’s history—once upon a distant time, after all, the earth only housed prokaryotes, while one peculiar Holocene species can now sit at a typewriter and pontificate about them. But the pattern dissolves upon close inspection. Most structural complexity entered in a grand burst at the Cambrian explosion, and the history of Phanerozoic life since then has largely been a tale of endless variation upon a set of *Baupläne*. We may discern a few “vectors” of directional change—thickening and ornamentation of shells among prey species while predators evolve more efficient weaponry (though this pattern has its punctuational aspects as well; see Vermeij 1977; Signor and Brett 1984)—but these are scarcely the stuff of progress in its usual sense. Nor can we view our own recently evolved consciousness as the end (both in time and *telos*) of a continuous upward march—for we are one peculiar sideline of an odd arboreal group in a class that would still be living as small and marginal creatures had some external cause not intervened to extinguish the dinosaurs (who were not, themselves, on the move toward any form of consciousness).

Progress is not merely a deep cultural bias of Western thought (Bury 1920; Nisbet 1980), it is also (and perhaps primarily for this reason) the explicit expectation of all deterministic theories of evolutionary mechanism that have ever achieved any popularity, from Darwinian selection to Lamarckism to orthogenesis. I do not, of course, mean progress as an unreversed, unilinear

march up the chain of being; Darwin did away with this silly notion forever. But even Darwinism anticipates that an imperfect, irregular, but general ascent should emerge from all the backing and forthing inherent in a theory based on a principle of local adaptation to changing circumstances. Darwin expected this kind of irregular progress—even within his theory of local adaptation—for two basic reasons: because competition regulates the history of life (by the metaphor of the wedge, *vide infra*) and better forms therefore prevail, and because biomechanical improvement is one mode of local adaptation, and organisms so constituted should persist longer and accumulate their patrimony through time. Thus, Darwin wrote (1859, p. 345):

The inhabitants of each successive period in the world's history have beaten their predecessors in the race for life, and are, insofar, higher in the scale of nature; and this may account for that vague yet ill-defined sentiment, felt by many paleontologists, that organization on the whole has progressed.

And all the great architects of the modern synthesis, especially Julian Huxley, were deeply concerned with the idea of progress and found explicit ways to incorporate its expectation into their accounts, often at great length (Simpson 1949; Huxley 1953; Stebbins 1969; Rensch 1971; Dobzhansky 1972). (Gary Vermeij, reviewing the first version of this paper, commented that progress itself, as a hopelessly vague and culture-laden term, should be expunged and replaced with something less encumbered, and perhaps even operational, such as "improvement" or "escalation." It is particularly revealing, in the light of the evident justice of Vermeij's suggestion, that progress continues to obsess evolutionists and that all the great synthesists of our century made its explication a major goal of their general writing. Perhaps we may best put the issue to rest by showing that, since tiers of time remove any lingering rationale, only culture and tradition can remain as bulwarks for regarding "progress" as the most general vector of life's history.)

I believe that our failure to find any clear vector of fitfully accumulating progress, despite expectations that processes regulating the first tier should yield such advance, represents our

greatest dilemma for a study of pattern in life's history. I shall call it the *paradox of the first tier*. In principle, two types of solutions might resolve this paradox (both, I suspect, with considerable validity). Perhaps, first of all, processes at the first tier do regulate life's history (as Darwinian tradition assumes), but we have been wrong about the nature of these processes—and that an appropriate revision will no longer yield an expectation of progress (which may never have had any deep justification beyond culturally conditioned hope in any case). Only in this context can we understand the passion that surrounds some contemporary debates about the first tier—particularly the challenge to competition's hegemony as the regulator of diversity, structuring agent of communities, and motor of change. (See Hutchinson [1959] and Dawkins and Krebs [1979] for the classic statement and its macroevolutionary extrapolation; and Simberloff [1983, 1984] for its sharp critique.) Simberloff, I think, is correct when he writes (1984, p. 22): "Still to be explained is why competition dominates ecological thinking, given the paucity of hard data to support it. The main reason, it seems, is the strong philosophical and religious appeal of the idea that something keeps nature in balance." Believe me, it is a pleasure to sit back, sip a beer, and watch something evoke more passion than punctuated equilibrium.

The second solution holds that forces of the first tier may indeed yield fitful progress, but that distinct processes at the second and third tiers reverse, dilute, or undo whatever the first tier can accumulate. This paper is dedicated to a defense of this second solution to the paradox of the first tier and therefore to what Maynard Smith (1984) has celebrated, in his quintessentially English metaphor, as the return of paleontology to the high table of evolutionary theory.

### III. Life at the Second Tier: Partisan Perspectives on a Decade of Punctuated Equilibrium

Punctuated equilibrium is a theory for the second tier—it studies the deployment of species and the origin of trends in normal geological times between episodes of mass extinction (Eldredge and Gould [1972] for the original statement; Gould and Eldredge [1977] and Gould [1982b] for later developments). It is neither a

theory about macromutation at the first tier nor a statement about mass extinction at the third—although in a more abstract sense, it embodies a general philosophy of change that has opened many minds to punctuational arguments at other levels (Gould 1984a); in this fruitful pluralism I take great delight, whatever may eventually happen to the specific hypothesis of punctuated equilibrium itself.

In developing the idea of punctuated equilibrium, Eldredge and I wanted to reverse a situation that had placed paleontology into a kind of intellectual black hole—an inability to refute its own central theory from within. This theory—phyletic gradualism—equated evolutionary change with continuous transformation in phyletic lines and subtly denied meaning to the evident (I would say predominant) punctuational pattern of stasis within species and geologically abrupt appearance of derived species. As such, it stymied our profession by imposing a lethargy upon evolutionary studies. Examples of continuous phyletic transformation are rare, while the theory of phyletic gradualism denied biological meaning to the more common observations that might have refuted it: abrupt appearance (dismissed as the artifact of an imperfect fossil record) and stasis (more subtly disregarded as “no data” in the light of an expectation for change). In our standard model of scientific progress, theories arise from new and unexpected observations. Punctuated equilibrium holds the curious status of a theory that simply promoted to meaningfulness the oldest observation of a profession—the literal appearance of the punctuational pattern, acknowledged at least since Cuvier.

I raise these two central points about punctuated equilibrium—its status as a theory of the second tier, and its solid basis in observation—because many critiques (e.g., Stebbins and Ayala 1981; Levinton 1983; Schopf and Hoffman 1983) have failed to understand them for various reasons, and because the role of punctuated equilibrium as a theory of macroevolution, and as a partial solution to the paradox of the first tier, relies upon them.

1. The radical implications of punctuated equilibrium all reside at the second tier. Many neontologists have been unable to break a long, historically conditioned habit of analyzing all

evolutionary propositions in terms of processes at the first tier of generations and populations during ecological moments. Thus, they have taken punctuated equilibrium and proclaimed it either incorrect because they misunderstand it as a theory of macromutation (Mayr 1982) or unoriginal because they do understand its statement for the first tier and properly recognize it as proposing nothing new about the mechanism of speciation (Jones 1981; Stebbins and Ayala 1981; Ayala 1983).

Punctuated equilibrium has never tried to say anything new about how speciation occurs at the first tier. Its original formulation, after all (Eldredge and Gould 1972), is little more than an attempt to show how the most orthodox version of Mayr’s peripatric theory scales properly into geological time. Thus, I confess that I rage inside when people tell me that we misunderstood ideas of scaling and that our “punctuations” are an ecologist’s gradualism. Our theory is rooted in this very recognition—in pointing out that our predecessors had scaled improperly in assuming that ecological gradualism extrapolated to phyletic continuity, and in arguing instead that the proper geological extension of peripatric speciation is punctuated equilibrium.

While I am at the confessional and in an uncharacteristically pugnacious mood, let me vent one more frustration at some critics. If the theory of punctuated equilibrium is so unoriginal (Levinton 1983, p. 113), so trivial and untestable (Gingerich 1984), so derivative (Penny 1983), then why in heavens name have they spent so much time and passion commenting upon it? People are not, after all, so stupid and gullible. Even my vaunted “literary pyrotechnics” (Halstead 1984, p. 40) could not command attention for a set of ideas with no content, originality, or promise. Punctuated equilibrium has evoked such a lively response because it has something to say. I rest my entire case upon the wonderful comments of two severe critics who understand deeply what we are trying to do—on Rhodes’s (1984) documentation of the utility of punctuated equilibrium (whatever its eventual truth value) as a hypothesis of broad implication that has inspired a multitude of empirical studies within paleontology and much fruitful extension into related fields, and on Maynard Smith’s (1984) delineation of the im-

portant issues that punctuated equilibrium raises for the central logic of evolutionary theory.

The radical implications of punctuated equilibrium arise from its primary role as a theory about trends at the second tier. It follows Mayr (1963) in moving speciation from a peripheral luxury for the production of diversity following progressive change by phyletic evolution (anagenesis) to a central role in constructing evolutionary novelty. But Mayr failed to grasp the geological implications of peripatry (1963, ch. 19) and continued to anticipate gradual phyleticism for the second tier. In arguing that most evolutionary change occurs during geologically rapid speciation and not during the long history of lineages, punctuated equilibrium holds that trends must be interpreted as the differential success of species, not as the history of change in phyletic lines. Punctuated equilibrium breaks the continuity of evolutionary explanation by arguing that the immediate adaptations of organisms within populations are not the only stuff of long-term evolution. We require a new level of analysis residing irreducibly at the scale of macroevolution. Speciation supplies the raw material of change; the sorting of species (differential success) at the second tier determines the direction of change (trends).

From this bounded independence (or decoupling [Stanley 1979]) flows the most controversial proposal of all: that the reasons for differential success of species, the motor of trends, lie irreducibly at the level of species and their behavior as higher-order individuals (Gould 1982a; Vrba and Eldredge 1984). Species prevail in trends either because they persist longer than others or because they speciate more often. If the reasons for this prevalence reduce to Darwinian struggles of organisms (extended persistence as a result of competitive success, for example), then we have only a description at the second tier, not a causal theory. But if the differential success of species either depends upon such irreducible properties of populations as their propensity to speciate ("species selection" in its causal sense, see Gould [1982a] and Maynard Smith [1983]), or if the reasons for success do arise from the struggle of organisms but translate to different properties at the level of populations (Vrba's "effect hypothesis"), then we cannot avoid a direct analysis of macroevolution in terms

of species as higher-order individuals. We must then reformulate Darwinism in a hierarchical manner, recognizing separate but interacting levels of selection (and other processes) for genes, organisms, demes, species, and monophyletic clades; we can no longer, as Darwinian tradition dictates, view evolution as the struggle of organisms for differential reproductive success within populations.

I am, in my own biased way, persuaded that punctuated equilibrium has a high (I would say predominant) relative frequency as an evolutionary pattern for the history of species. I am not as convinced that it usually requires an irreducible analysis at the species level. This is the great open question that the first decade of punctuated equilibrium has produced. The hierarchical model is sound in logic and extensive in implications for a revised view of life's history. But if 98% of events do occur at the good old Darwinian level of organisms, and only 1 or 2% require genic or species selection, then traditional views prevail. The issue, as always in natural history, is relative frequency, not occasional occurrence or validity in principle. The welter of proposals both for independence and for non-Darwinian processes at the genic level (Doolittle and Sapienza 1980; Orgel and Crick 1980; Dover 1982) convince me that hierarchy is important and that a major agenda for evolutionary theory before the millennium must be its explicit development.

2. The firm foundation of punctuated equilibrium in observation. Given the fossil record's notorious imperfection, the primary empirical test of punctuated equilibrium must lie in the study of stasis and its relative frequency (although punctuations have been found and dissected, with fascinating insights about the nature and extent of intrapopulational variation during rapid transitions, in especially favorable stratigraphic settings—see Williamson [1981]).

My greatest satisfaction, in the midst of so much unresolved debate about other aspects of the theory, lies in our success with documenting the frequency and importance of stasis (for the structure of evolutionary theory before punctuated equilibrium scarcely permitted its recognition as a phenomenon worthy of note; it stood primarily as nonreported nonevidence of evolution). Some critics have stated or implied (Lev-

inton 1983; Schopf and Hoffman 1983) that stasis either remains undocumented or dissolves into ambiguity or gradualism upon further study (one critic has even called stasis “zero-rate gradualism,” a curious example of Newspeak and the hold of theory upon observation). But consider only the most extensive meeting arranged since punctuated equilibrium to consider the empirical basis of macroevolutionary patterns in paleontological case studies (Ager et al. 1983; Lister 1984). Results were numerous and varied, but a strong relative frequency for stasis clearly emerged. (R. Fortey, for example, estimated that 90% of events in the evolution of trilobites occur in the punctuational mode.) The “churning” of the genome on a time scale far shorter than the usual duration of paleospecies has been cited as a refutation of stasis (Schopf 1981), but this important conclusion of molecular biology only makes morphological stasis more interesting (Wake et al. 1983), since it connotes a discordance of pattern at different hierarchical levels (as we have long known exists, for example, between the quasi-clocklike accumulation of fixed neutral mutations and rates of adaptive phenotypic change). It would stand as a refutation only if the genome were fundamental and all else derivative—and I (with all paleobiologists I trust) reject such a destructive reductionism.

In a decade of empirical work, we have begun to discern both taxonomic and ecological patterning in the relative frequency of rates and modes. Gradualism is more common in oceanic microplankton (Malmgren and Kennett 1981; several articles in *Paleobiology*, vol. 9, no. 4); punctuated equilibrium predominates in benthic invertebrates, and not as an artifact of imperfection because the documentation of stasis only requires adequate sampling, not continuity (see other putative patterns in Johnson [1982] and Lister [1984]). These differences in relative frequency are not a refutation of punctuated equilibrium (low relative frequency in all cases would, of course, be a disproof), but a sign of its value as a hypothesis. We could not even ask such questions before punctuated equilibrium because stasis was ignored as nonevidence.

Among its implications for evolutionary theory, punctuated equilibrium proposes a resolution for the paradox of the first tier. If trends are the extrapolated adaptive struggles of organ-

isms, then progress should accumulate fitfully through time. As its major contribution to evolutionary pluralism, punctuated equilibrium greatly expands the range of explanation for trends. If trends are often irreducible phenomena of the second tier, then we immediately lose our expectation of progress for the history of morphology. If features spread through clades by nonadaptive hitchhiking upon the greater propensities for speciation in populations carrying them—or, to cite a nonselective explanation, merely by the good luck of survival when mass extinction removes other incumbent groups for reasons unrelated to structural superiority—then we have lost our rationale for expecting that trends in morphology should be progressive. The paradox of the first tier dissolves because the first tier does not regulate trends at the second.

Until Alvarez’s asteroid and Raup and Sepkoski’s periodicity of mass extinction, I thought that punctuated equilibrium would provide, in itself, an adequate resolution for the paradox of the first tier. I no longer believe this. New data and ideas on mass extinction have added an argument at the third tier, at least as important (and probably more so) in dissolving our expectation of progress. Punctuated equilibrium proposes that new explanations for trends at the second tier contain no expectation of progress. If such trends have a high relative frequency, the paradox disappears. New views on mass extinction argue that, whatever happens at the second tier, mass extinctions are sufficiently frequent, intense, and different in impact to undo and reset any pattern that might accumulate during normal times.

#### IV. Establishment of the Independence of the Third Tier

As ideas whose time may have come, mass extinction shares an interesting property with punctuated equilibrium. Neither represents a new discovery; both involve the reluctant acceptance of an acknowledged literal pattern that deep biases of Western thought had led us to mitigate or deny. Just as we have long known about stasis and abrupt appearance, but have chosen to fob it off upon an imperfect fossil record, so too have we long recognized the rapid, if not sudden, turnover of faunas in episodes of mass extinction. We have based our geological alphabet,

the time scale, upon these faunal replacements. Yet we have chosen to blunt or mitigate the rapidity and extent of extinctions with two habits of argument rooted in uniformitarian commitments. First, we have deemphasized some extinctions by drawing dubious phyletic connections across the boundaries. Second, and more important, we have tried to distribute these events more evenly in time by seeking evidence for slow declines before boundaries and reduced peaks of extinction at the terminations themselves. In short, we have tried to place mass extinctions into continuity with the rest of life's history by viewing them as only quantitatively different—more and quicker of the same—rather than qualitatively distinct in both rate and effect.

Seilacher's reinterpretation of the Ediacara fauna illustrates the first bad habit and its potential rectification (Seilacher 1983; commentary in Gould 1984b). Most Ediacaran animals have traditionally been linked by ties of homology, if not direct ancestry, with major Phanerozoic phyla (Glaessner 1961), thus spreading out the Cambrian explosion and identifying the Precambrian-Cambrian transition as the only era boundary without a major extinction. But Seilacher argues that morphological resemblances of Ediacaran and later creatures are superficial only; close examination precludes sufficiently similar function for reasonable phyletic ties. Ediacaran "medusoids," for example, have concentric and radial structures, but in positions reversed with respect to modern jellyfish (radial grooves at the periphery, concentric channels near the center), and therefore impossibly positioned for feeding and locomotion as performed by Phanerozoic coelenterates. Ediacaran "alcyonarians" do not bear separate stems that could house polyps with adequate access to feeding currents; they form a continuous, quilted structure and could not work as a modern soft coral. Instead, Seilacher finds a different but common structure among Ediacaran animals, marking them as a potentially coherent group that became extinct without metazoan descendants. They are pancake- or ribbon-like, perhaps quilted to provide strength at such a tenuous size and shape. They may represent a unique fauna, built under the other structural principle for attaining large size in the face of declining surface/volume ratios (not internal complexity for increasing surface area, as

in nearly all modern, roughly globular large creatures, but a change in external shape to insure that nothing inside is very far from the outside surface).

But the potential revolution in our ideas of mass extinction lies more in a reversal of the second habit of argument. I cannot begin to review this literature here; our technical and popular press have been flooded with its fruitful results (*Nature*, vol. 308, April 19, 1984; *Discover*, May 1984). We are, I think, finally on the verge of developing a general theory for mass extinction. Theories are heuristic devices: they guide perception and allow us to pose testable questions. Without adequate theory, we are condemned to flounder. In short, the new ideas have validated the notion of catastrophic termination (despite all the proper nuances of potentially multiple and tolerably spaced catastrophes in cometary showers, and the important role of terrestrial factors in setting geological stages for the differential severity of extinctions). As a summary statement, identifying the third tier as distinct, we may say that mass extinctions are more *frequent*, more *rapid*, more *extensive in impact*, and more *qualitatively different in effect* than our uniformitarian hopes had previously permitted most of us to contemplate.

The new ideas have emerged as a fruitful marriage of paleobiological with geochemical and physical data. The famous iridium anomaly in sediments at the K-T boundary (originally at just three sites) led the Alvarez team to its bold conjecture about asteroidal impact (Alvarez et al. 1980), since stunningly confirmed by establishment of the K-T anomaly as worldwide, and then extended in generality by putative reports of similar iridium enhancements at several other extinction boundaries. Raup and Sepkoski (1982) had already noted the unanticipated distinctness (against background levels) of the five greatest mass dyings. A refined statistical analysis of Sepkoski's comprehensive data (the product of a decade of tabulation) then revealed an apparent 26 (or 30 [Raup, 1985]) ma periodicity of extinction (Raup and Sepkoski 1984; Sepkoski and Raup, 1985), and preliminary study of large impact craters suggests a regularity of similar spacing and phase (Alvarez and Muller 1984). Random asteroidal impacts no longer suffice, though iridium anomalies probably still re-

quire an extraterrestrial source (but see Officer and Drake 1985). Cometary impacts will also supply the iridium and might engender the same basic “killing scenario” of massive dust clouds and the natural analog to nuclear winter. Some weird and wonderful mechanisms for periodic cometary showers are now before us, including a previously unrecognized solar companion on an eccentric orbit that might come close enough every 26 or 30 ma to disturb the Oort cloud of comets and send several billion hurtling into the space of the inner planets. I would not bet much on the validation of Nemesis (or Siva, as I like to call our potential dark star [Gould 1984c])—but the idea is not laughable and it is eminently testable (several articles in *Nature*, vol. 311, Oct. 18, 1984). At least no one can ever again accuse paleontology of insipidity.

When new theories coordinate old observations in novel ways, I like to ask a basic question: What prevented such an integration before, or what biases constrained our thought (the stubbornest are those not explicitly recognized and therefore assumed as empirical truth)? The strongest constraints upon independent theories of macroevolution arise from the central postulate of the modern synthesis: that an adequate account of evolutionary processes may be sought in the struggles of individual organisms for enhanced reproductive success within populations. This form of strict Darwinism is reductionist in character (to organisms, though not to their atoms and molecules) and selectionist in mechanism. With respect to independence at the second tier, I have long argued that gradualism and adaptationism are the principal biases from the first tier that have impeded the development of an expanded, hierarchical form of Darwinism (Eldredge and Gould 1972; Gould and Lewontin 1979; Gould 1982a). The extrapolationist vision of extended struggle for existence within populations—the march of frequency distributions through time—is a powerful metaphor.

A different but equally pervasive assumption of Darwinism at the first tier has prevented our recognition of independence at the third tier of mass extinction: competition as regulator of diversity and motor of progress. Darwin expressed his commitment to competition in one of his most striking and celebrated images—the metaphor of the wedge:

Nature may be compared to a surface covered with ten-thousand sharp wedges . . . representing different species, all packed closely together and driven in by incessant blows, . . . sometimes a wedge of one form and sometimes another being struck; the one driven deeply in forcing out others; with the jar and shock often transmitted very far to other wedges in many lines of direction. (From *Natural Selection*—the “big book” from which Darwin abstracted the *Origin*. This passage is more vivid and striking than the version Darwin included in the *Origin*—see Stauffer [1975], p. 208.)

In the metaphor of the wedge, the world is full and new forms can prevail only by driving others out (“wedging,” as Darwin often called it). Larger scale replacement in the fossil record is extrapolated wedging as superior designs replace inferior models, species by species. In the geological chapters of the *Origin*, when Darwin was not bemoaning imperfection and extolling unobserved gradualism, he devoted most space to the predictions for wedging, particularly to the argument that extinction of higher taxa must be heralded by long preceding declines in diversity and geographic extent. Van Valen’s Red Queen (1973) is the latest metaphorical expression of extrapolated wedging: on the treadmill of competition, species must run all the time just to maintain their position.

The theory of periodic, catastrophic impact challenges this vision and suggests independence at the third tier. Competition may regulate the first tier and hone morphological adaptation. But species cannot prepare for an intermittent holocaust. If any predictable pattern regulates differential survival through mass extinctions, it can only operate by fortuitous exaptation (Gould and Vrba 1982). The causes of pattern at this scale are not reducible to natural selection at the first tier, as models of wedging assume. Most of the faunal relays and replacements that mark the history of life are probably noncompetitive; incumbent groups are removed and survivors capable of filling similar ecological roles (but previously unsuccessful at dislodging former occupants by competition) radiate. We need a new metaphor for the success of dinosaurs over therapsids and mammals over dinosaurs. In de-

bunking wedging (Gould and Calloway 1980) for its classic invertebrate example of clams versus brachiopods (by showing that the relay was not gradual wedging but differential response to the Permian debacle), I suggested Longfellow's "ships that pass in the night . . . only a signal shown and a distant voice in the darkness."

It goes almost without saying that such a theory of mass extinction would largely resolve the paradox of the first tier. If anything like progress accumulates during normal times (and punctuated equilibrium casts doubt even upon this proposition), the vector of advance may be derailed often and profoundly enough to undo any long term directionality.

## V. An Agenda for Paleobiology

Paleontologists will always do much of their work at the first tier: we must develop our basic data of taxonomy and reconstruction of environments and communities during ecological moments of the past. But the excitement of paleobiology in the world of ideas lies in the theories it has developed at the second tier of sustained trends during millions of years in normal times and the third tier of mass extinction. We have reclaimed our proper role among the evolutionary sciences—as generators of testable and irreducible theories about pattern in the history of life, not passive recordkeepers of a phenomenology fully explained at the first tier.

Punctuated equilibrium has provided a controversial framework for independence at the second tier. Much remains to be done, and affirmed or disproved empirically, but the theory's logic is sound and now reasonably well developed. We must learn, for example, how often ancestors persist after apparent punctuations—for the pattern of "punctuated gradualism" (Malmgren et al. 1983), which should be called "punctuated anagenesis," refutes the central prediction that evolution is concentrated in events of branching speciation, while affirming the punctuational style of change. We need to explore further the emerging patterns of differential relative frequency along taxonomic and ecological lines. We must develop and apply tests to distinguish true species selection from extrapolatable effects of classical Darwinian struggle among organisms.

Yet I suspect that the major excitement with-

in paleobiology will now shift to the third tier, where theories are so novel, testable predictions so clear, and implications so profound. For starters, the post-Permian periodicity presents an obvious challenge and a key prediction: can it be extended back into the Paleozoic (where stage lengths are now too long and uncertainties of dating too numerous to apply it); will the two post-Permian "holes" (points on the recurrence without associated extinctions for now) be filled? For second place, the complex consequences of impact and the contributions of terrestrial factors must be worked out. We don't even have a clear and appropriate killing scenario; the cold darkness of dust clouds might not suffice or might represent just one of numerous effects. How do the physical, chemical, and meteorological effects of impact alter our biosphere, atmosphere, and lithosphere? How can we integrate collateral fluctuations in terrestrial conditions with the primary triggers of impact? Does temperature play a role beyond the direct alterations wrought by catastrophes (Stanley 1984)? And what about the independent forces of plate tectonics? We shall probably find a causal link in the coexistence of Pangaea with the granddaddy of all extinctions. I used to think that Pangaea was the primary cause of the Permian debacle (Schopf 1974); I now suspect that it was a terrestrial stage for maximal severity.

More generally, the quantitative theory of periodic, catastrophic impact challenges paleobiology to construct a general theory for shifting high-order taxonomic pattern in life's history. Some of life's general pattern must be regulated at the first tier (Signor and Brett 1984). But if we cannot extrapolate competition to make mass extinction just more of the same, then we will also need new theories based either on a "random" or a "different rules" model, and probably on a good deal of both. We are deluged with anecdotes about who does and doesn't get through mass extinctions. We must first test the random model that no causal order exists, and that bullets from heaven strike evenly spaced equipotential spheres. Failing this (and it may not fail), we must ask what rules regulate differential survival in mass extinction (see Jablonski and Bottjer 1983, for example) and, especially, how they differ from reasons for success in normal times (both in trends regulated by

punctuated equilibrium and at the Darwinian first tier of local selection). Jablonski, for example, has argued that species-rich clades may increase by species selection in normal times but fail differentially in mass extinction by the very properties—stenotopy, limited capacity for dispersal—that enhance speciation otherwise. Negative interaction between tiers and hierarchical levels must regulate much of life's stability, but we couldn't even pose the appropriate questions while we worked with reductionist models of the first tier alone (Gould 1982a).

Questions are bursting out all over; I could fill the rest of this issue with a list, if the editor would only give me space. Just one, as an example of what we can now ask. Consider the history of mollusks and echinoderms and its general pattern of marked reduction in class-level diversity and great expansion at lower taxonomic levels within surviving groups. I believe that this reduction of diversity and expansion at stable points of design—and not progress—is the major pattern of life's history, at least for marine invertebrates. Shall we accept the usual deterministic explanation that best designs survive (wedging again), and that we are dealing with "early experimentation and later standardization?" Such an explanation makes sense and is consistent with the behavior of stabilizing systems, as they trim their tails of diversity (.400 hitting in baseball has disappeared for the same basic reason [Gould 1983]; we are discussing an abstract and general property of systems). But perhaps we have been quite wrong; perhaps the random side of mass extinction produces the pattern under the most general constraint of evolving systems—their treelike topology, with irrevocable independence of lineages and resultant permanency of extinction. The simple first test: do the 20 or so higher taxa of extinct Paleozoic echinoderms disappear at regular Paleozoic boundaries of mass dying, still to be adequately determined? If so, do they die at close to maximal diversity of species or do they decline slowly before their demise? And I haven't even mentioned all the questions raised by functional morphology.

We shall not be wanting for intellectual excitement before the millennium. We will probably have enough to keep us busy until the next barrage of comets. We have validated a different

metaphor for change—the punctuational style of stability actively preserved but episodically disrupted, with its basic corollary that structure is intrinsic in nature, not just a fleeting incarnation along a path of continuous alteration (punctuated equilibrium at the second tier, mass extinction at the third). We have affirmed the theoretical independence of our discipline by recognizing hierarchies of structure and tiers of time—and we have set the basis for fruitful junction with neontology at the first tier by studying interactions between levels and by recognizing the value of analogy when extrapolation doesn't work and causal unity when it does. I think that we have also resolved the paradox of the first tier.

*Nature* had the nerve to write of us in 1969 (anonymous, p. 903): "Scientists in general might be excused for assuming that most geologists are palaeontologists and most palaeontologists have staked out a square mile as their life's work. A revamping of the geologist's image is badly needed." But if the solar companion exists, paleontology shall be the impetus for the greatest revision of cosmology, at least for our corner of the heavens, since Galileo. And if it doesn't, *tant pis*. Our own star is riding high enough.

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