Punctuated equilibrium comes of age

Stephen Jay Gould & Niles Eldredge

The intense controversies that surrounded the youth of punctuated equilibrium have helped it mature to a useful extension of evolutionary theory. As a complement to phyletic gradualism, its most important implications remain the recognition of stasis as a meaningful and predominant pattern within the history of species, and in the recasting of macroevolution as the differential success of certain species (and their descendants) within clades.

But orderly extensions, implicit in the undeveloped logic of our original argument, fueled the useful growth of punctuated equilibrium to fruitful adulthood. (We now realize how poorly we initially grasped the implications of our original argument; we thank our colleagues, especially S. M. Stanley and E. S. Vrba, for developing several extensions). We originally focused on tempo, but more important theoretical arguments flowed from implications concerning evolution’s mode—particularly the causes surrounding our two major claims for equilibrium, or stasis of established species, and the need to reformulate macroevolution, notably the key phenomenon of trends, as an accumulation of discrete speciation events treated as entities rather than undefined segments of continua—a subject encompassed by debate about species selection or species sorting.

Punctuated equilibrium and macroevolution

Stasis and Its meaning. We opened our original paper with a section on what philosopher N. R. Hanson called “the cloven hoofprint of theory,” or the structuring of all supposedly objective observation by expectations of prevailing general views. Stasis, as palpable and observable in virtually all cases (whereas rapid speciation is usually, but not always, elusive), becomes the major empirical ground for studying punctuated equilibrium. Putting together the philosophical insight of inductible theoretical bias, with the empirical theme of the tractability of stasis, we devised a motto: “Stasis is data.” For no bias can be more constraining than invisibility—and stasis, inevitably read as absence of evolution, had always been treated as a non-subject.

How odd, though, to define the most common of all paleontological phenomena as beyond interest or notice! Yet paleontologists never wrote papers on the absence of change in lineages before punctuated equilibrium granted the subject some theoretical space. And, even worse, as paleontologists did not discuss stasis, most evolutionary biologists assumed continual change as a norm, and didn’t even know that stability dominates the fossil record. Mayr has written: “Of all the claims made in the punctuationalist theory of Eldredge and Gould, the one that encountered the greatest opposition was that of pronounced stasis as the usual fate of most species,” after having completed the phase of origination... I agree with Gould that the frequency of stasis in fossil species revealed by the recent analysis was unexpected by most evolutionary biologists.”

As the most important change in research practice provoked by punctuated equilibrium, stasis has now exited from its closet of non-definition to become a subject of quantitative investigations in all major fossil groups—from microfossils (27,000 measured specimens from 400 closely spaced samples spanning 8 million years in the latter study), to molluscs (35,000), to mammals (35,000). Although punctuated equilibrium deals directly only with stability of species through time, the higher-level analogue of non-trending in larger clades has also graduated from an undefined non-subject to a phenomenon worth documenting. Moreover, because species often maintain stability through such intense climatic change as glacial cycling, stasis must be viewed as an active phenomenon, not a passive response to unaltered environments. Many leading evolutionary
theorists, while not accepting our preference for viewing stasis in the context of habitat tracking or developmental constraint, have been persuaded by punctuated equilibrium that maintenance of stability within species must be considered as a major evolutionary problem.

Macroevolution as a problem in species sorting. If punctuated equilibria provoked a shift in paradigms for macroevolutionary theory (see ref. 15 for a defence of this view), the main insight for revision holds that all substantial evolutionary change must be recognised as higher-level sorting based on differential success of certain kinds of stable species, rather than as progressive transformation within lineages (see Eldredge in a taxon versus transformational views of evolution; Simpson, however, in the canonical palaeontological statement of the generation before a punctuated equilibria, had attributed 90% of macroevolution to the transformational mode, and only 10% to speciation). Figure 1, our original diagram of punctuated equilibria, shows how a trend may be produced by differential success of certain species without directional change in any species following its origin.

Darwin's theory of natural selection locates the causality of evolutionary change at one domain on one level: natural selection operating by struggle among individual organisms for reproductive success. Given Darwin's crucial reliance upon phyletic uniformity for extrapolating this mode of change to encompass all magnitudes through all times, the interposition of a level for sorting among stable species breaks this causal reduction and truth, in Stanley's felicitous term, "decouples" macro-evolution from microevolution. Decoupling is not a claim for the falseness or irrelevancy of microevolutionary mechanisms, especially natural selection, but a recognition that darwinian extrapolation cannot fully explain large-scale change in the history of life.

The main point may be summarised as follows. Most macro-evolution must be rendered by asking what kinds of species within a clade do better than others (speciated more frequently, survived longer), or what biases in direction of speciation prevailed among species within a clade. Such questions enjoin a very different programme of research from the traditional "how did natural selection within a lineage build substantial adaptation during long stretches of time?" The new questions require a direct study of species and their differential success; older queries focused downward upon processes within populations and their extrapolation through time. Darwin's location of causality in organism must be superseded by a hierarchical model of selection, with simultaneous and important action at genic, organism and taxic levels. Williams, who so stoutly defended classical Darwinism against older, invalid, and very different forms of group selection, now acknowledges the importance of such clade selection in macroevolution. Punctuated equilibrium has been used as a central concept in the development of hierarchy theory in evolutionary biology.

Implications. Any theory with a claim to novelty in broad perspective must enlighten old problems and suggest extensions. The speciational view of macroevolution, which does not strictly require punctuated equilibrium, but which was nurtured and has thrived in its context, requires a reformulation of nearly all macroevolutionary questions. For example, so-called living fossils, once treated as lineages rendered static by optimal adaptation, unusually stable environment, or lack of genetic variation, should be reconceptualised as members of groups with unusually low speciation rates, and therefore little opportunity to accumulate change. (We have no evidence that the species of "living fossil" groups are particularly old. For example, the western Atlantic horseshoe crab, Limulus polyphemus—the type example of the phenomenon—has no fossil record at all, whereas the genus can only be traced to the Miocene.)

Going further, the entire tradition of expressing evolutionary change in darwin units (where 1 darwin equals character change by a factor of e in 1 million years) makes no sense in a speciational context. (If a lineage goes from species A to D in 10

FIG. 1 Three-dimensional sketch contrasting a pattern of relative stability (A) with a trend (B), where speciation (dashed lines) is occurring in both major lineages. Morphological change is depicted here along the horizontal axes, while the vertical axis is time. Though a retrogressive pattern of directional selection might be fitted as a straight line in (B), the actual pattern is stasis within species, and differential success of species exhibiting morphological change in a particular direction. For further explanation, see ref. 1.
rates would fare just as well as groups with equally lower rates. But extinction intensities vary greatly, and the geological record features episodes of high dying, during which extinction-prone groups are more likely to disappear, leaving extinction-resistant groups as life's legacy. Valentine concludes that "these cladecharacteristic rates are of course not adaptations per se, but effects flowing from clade properties that were established probably during the early radiations that founded the clades."

The most exciting direct extensions of punctuated equilibrium now involve the study of correlated punctuational events across taxa, and the ecological and environmental sources of such cohesion. Eminent testable are Vrba's" turnover-pulse hypothesis of evolution concentrated in punctuational bursts at times of worldwide climatic pulsing, one of which, about 2.5 million years ago, may have stimulated the origin of the genus Homo; and Brett's" hypothesis of "coordinated stasis" for the structuring of major palaeontological faunas. What might be the ecological source of such striking coherence across disparate taxa through such long times?"24

The empiric of punctuated equilibrium
Like all major theories in the sciences of natural history, including natural selection itself, punctuated equilibrium is a claim about relative frequency, not exclusivity. Phyletic gradualism has been well documented, again across all taxa from microfossils to mammals.5,52 Punctuated equilibrium surely exists in abundance, but validation of the general hypothesis requires a relative frequency sufficiently high to impart the predominant motif and signal to life's history. The issue remains unsettled, but we consider (in our biased way) that four classes of evidence establish a strong putative case for punctuated equilib-rium in this general sense.

Individual cases. Examples of stasis alone (cited earlier) and simple abrupt replacement, although conforming to expectations of punctuated equilibrium, are not direct evidence for our mechanism: for stasis might just be a full in anagenetic gradualism (though pervasive stasis for long periods in all species of a fauna (a common finding) would require special pleading from gradualists), and replacement might represent rapid transformation without branching, or migration of a distant (phyletic or geographic) relative rather than evolution in situ. A good test of punctuated equilibrium requires (in addition to the obvious need for documented rapidity in an interval known to be sufficiently short) both a phyletic hypothesis to assert sister-group relationship of the taxa involved, and survival of putative ancestors to affirm an event of true branching rather than rapid phyletic transformation.

Given these stringent requirements, and in the light of such an imperfect fossil record, we are delighted that so many cases have been well documented, particularly in the crucial requirement of ancestral survival after punctuated branching.44,45 Williamson's discovery of multiple molluscan speciation events in isolated African lakes, with return of ancestral lineages upon reconnection with parental water bodies, has been most widely discussed, and disputed (although all accept the punctuational pattern). Cheetham's elegant and meticulously documented study of evolution in the bryozoan Metrarabdotois from Tertiary strata of the Caribbean is particularly gratifying (Fig. 2) in the number of purely punctuational events, the full coverage of the lineage, and the unusual completeness of documentation, especially as Cheetham began his study expecting to reconfirm a gradualistic interpretation (writing to McKinney: "The chronocline I thought was represented... is perhaps the most conspicuous, arguably the most conspicuous, of the studies, which shows that the supposed line members largely overlap each other in time. Eldredge and Gould were certainly right about the danger of stringing a series of chronologically isolated populations together with a gradualist's expectations.")

On the subject of punctuational corrections for received gradualistic wisdom, Prothero and Shubin have shown that the most 'firmly' gradualistic part of the horse lineage (the general, and false, exemplar of gradualism in its totality), the Oligocene...
transition from *Mesoshippus* to *Miohippus*, conforms to punctuated equilibrium, with stasis in all species of both lines, transition by rapid branching rather than phyletic transformation, and stratigraphic overlap of both genera (one set of beds in Wyoming has yielded three species of *Mesoshippus* and two of *Miohippus*, all contemporaries). Prothero and Shubin conclude: "This is contrary to the widely-held myth about horse species as gradually-varying parts of a continuum, with no real distinctions between species. Throughout the history of horses, the species are well-marked and static over millions of years. At high resolution, the gradualistic picture of horse evolution becomes a complex bush of overlapping, closely related species."

**Relative frequencies.** Elegant cases don't make punctuated equilibrium any more than a swallow makes a summer, but there are a growing number of reports documenting an overwhelming relative frequency (often an exclusivity) for punctuated equilibrium in entire groups or faunas. Consider the lifetime testimonies of taxonomic experts on microfossils on brachiopods and on beetles. Fortey has concluded for trilobites and graptolites that the gradualistic mode occurs especially in pelagic or pelagic forms, but accounts for 10% or less of observations of phyletic change, and is relatively slow.

Other studies access all available lineages in entire faunas and assert the dominance of punctuated equilibrium. Stanley and Yang found no gradualism at all in the classic Tertiary molluscan sequences of the Gulf and Atlantic Coasts. With the exception of *Gryphaea*, Hallam detected no phyletic change in shape (but only size) in any Jurassic bivalve in Europe. Kelley documented the prevalence of punctuation for molluscs in the famous Maryland Miocene sequence, and Vrbka has done the same for African boids. Even compilations from the literature, so greatly biased by previous traditions for ignoring stasis as non-data and only documenting putative gradualism, grant a majority to punctuated equilibrium, as in Barnovsky's compendium for Quaternary mammals, with punctuated equilibrium "supported twice as often as phyletic gradualism... the majority of species considered exhibit most of their morphological change near a speciation event, and most species seem to be discrete entities." When controlled studies are done by one team in the field, punctuated equilibrium almost always seems to predominate. Prothero "examined all the mammals with a reasonably complete record from the Eocene-Oligocene beds of the Big Badlands of South Dakota and related areas in Wyoming and Nebraska... With one exception (gradual dwarving in the orendoct *Mammothus*), we found that all of the Badlands mammals were static through millions of years, or speciated abruptly (if they changed at all)."

**Inductive patterns.** Even more general inductive patterns should be explored as criteria. Stanley proposes a series of tests, all carried out to punctuated equilibrium's advantage. Others suggest that certain environments and ecologies should be conducive to one preferred mode along the continuum of possibilities. Johnson suggests that punctuated equilibrium should dominate in the benthic environments that yield most of our fossil record, while gradualism might prevail in pelagic realms. Shubin opposes the concept altogether but not unreasonably asserts that punctuated equilibrium may prevail in unstable environments, gradualism in stable regimes.

**Tests from living organisms.** Distinct evolutionary modes yield disparate patterns as results; punctuated equilibrium might therefore be tested by studying the morphological and taxonomic distributions of organisms, including living faunas. Several of Stanley's tests use modern organisms, and other criteria from fossils should be explored—especially the biometric discordance or orthogonality, favourable to punctuated equilibrium and actually found where investigated, of within and between species trends.

Cladistic patterns should provide a good proving ground. Avise performed an interesting and much quoted test, favourable to gradualism, by comparing genetic and morphological differences in two fish clades of apparently equal age and markedly different speciation frequencies. But as Mayden argued, this test was wrong in its particular case, and non-optimal as a general procedure: a better method would compare cladistic sister groups, guaranteed by this status to be equal in age. Mindell et al. have now performed such a test on the reptilian genus *Sceloporus* and on allozymic data in general, and have validated punctuated equilibrium's key claim for positive correlation of evolutionary distance and speciation frequency. Leman and Freeman's interesting proposal for additional cladistic tests cannot be sustained because they must assume that unbranched arms of their cladograms truly feature no speciation events along their routes, whereas numerous transient and extinct species must populate most of these pathways. Wagner has developed a way of estimating rapidly branching speciation versus gradual speciation or transformation from cladograms, and his initial results favour predominant rapid branching in Palaeozoic gastropods.

**Difficulties and prospects.** Many semantic and terminological muddles that once impeded resolution of this debate have been clarified. Opponents now accept that punctuated equilibrium was a novel and unorthodox theory, and that stasis does not signify rock-hard immobility, but fluctuation of little or no accumulated consequence, and temporal spread within the range of geographic variability among contemporary populations—by Stanley's proper criteria, so strikingly validated in his classic study. We trust that everyone now grasps the centrality of relative frequency as a key criterion (and will allow, we hope, that enough evidence has now accumulated to make a case, if not fully prove the point).

Evolutionary biologists have also raised a number of theoretical issues from their domain of microevolution. Some, like the frequency of sibling speciation, seem to us either irrelevant or untroublesome as a bias against, rather than for, our view (as we then underestimate the amount of true speciation from palaeontologically defined morphospecies, and such an underestimate works against punctuated equilibrium). Others, like the potential lack of correspondence between biospecies and palaeontological morphospecies, might be worrisome, but available studies, done to assess the problem in the light of punctuated equilibrium, affirm the identity of palaeontological taxa with true biospecies (see Jackson and Cheetah on broozoan species, and Michaux on palaeontological stasis in gastropod morphospecies that persist as good genetic biocpecies).

But continuing unhappiness, justified this time, focuses upon claims that speciation causes significant morphological change, for no validation of such a position has emerged (while the frequency and efficacy of our original support of the notion, Mayr's "genetic revolution" in peripheral isolates, has been questioned). Moreover, reasonable arguments for potential change throughout the history of lineages have been advanced, although the empiries of stasis throws the efficacy of such processes into doubt. The pattern of punctuated equilibrium exists (at predominant relative frequency, we would argue) and is robust. *Eppur si muove*; but why then? For the association of morphological change with speciation remains as a major pattern in the fossil record.

We believe that the solution to this dilemma may be provided in a brilliant but neglected suggestion of Futuyma. He holds that morphological change may accumulate anywhere along the geological trajectory of a species. But unless that change be locked up by acquisition of reproductive isolation (that is, speciation), it cannot persist or accumulate and must be washed out during the complexity of interdigitation through time among varying populations of a species. Thus, species are not special because their origin permits a unique moment for instigating change, but because they provide the only mechanism for protecting change. Futuyma writes: "In the absence of reproductive
isolation, differentiation is broken down by recombination. Given reproductive isolation, however, a species can retain its distinctive complex of characters as its spatial distribution changes along with that of its habitat or niche... Although speciation does not accelerate evolution within populations, it provides morphological changes with enough permanence to be registered in the fossil record. Thus, it is plausible to expect many evolutionary changes in the fossil record to be associated with speciation. By an extension of the same argument, sequences of speciation are then required for trends: "Each step has had a more than ephemeral existence only because reproductive isolation prevented the slippage consequent on interbreeding with other populations... Speciation may facilitate anagenesis by retaining, stepwise, the advances made in any one direction." Futuyma's simple yet profound insight may help to heal the remaining rifts and integrate punctuated equilibrium into an evolutionary theory hierarchically enriched in its light.11,12

In summarizing the impact of recent theories upon human concepts of nature's order, we cannot now yet whether we have witnessed a mighty gain in insight about the natural world (against anthropocentric hopes and biases that always held us down), or just another transient blip in the history of correspondence between misperceptions of nature and prevailing social realities of war and uncertainty. Nonetheless, contemporary science has massively substituted notions of indeterminacy, historical contingency, chaos and punctuation for previous convictions about gradual, progressively predictable determination. These transitions have occurred in field after field; Kuhn's celebrated notion of scientific revolutions is, for example, a punctuational theory for the history of scientific ideas. Punctuated equilibrium, in this light, is only paleontology's contribution to a Zeitgeist, and Zeitgeists, as (literally) transient ghosts of an earlier time, should never be trusted. Thus, in developing punctuated equilibrium, we have either been too hasty and perchers to fashion, and therefore despise for history's sheath, or we had a spark of insight about nature's constitution. Only the punctuational and unpredictable future can tell...