Opus 200 - Stephen Jay Gould

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In my adopted home of Puritan New England, I have learned that personal indulgence is a vice to be tolerated only at rare intervals. Combine this stricture with two further principles and this essay achieves its rationale: first, that we celebrate in hundreds and their easy multiples (the Columbian quincentenary and the fiftieth anniversary of DiMaggio's hitting streak—both about equally important, and only the latter an unambiguous good); second, that geologists learn to take the long view.

This is my 200th essay in "This View of Life," a series begun in January 1974 (with never an issue missed). If once is an incident and twice a tradition, I now establish an indulgence for even multiples of 100 only. Essays must express the personal thoughts and prejudices of authors—for this has been the genre's definition ever since Montaigne. But I have tried not to abuse the bully pulpit of this forum to act as a shill for my own professional research and theorizing. Still, once in a hundred shouldn't subvert my *bonae fides*, so I indulge, as I did once before at my own centenary.

Essay 100 treated the Bahamian land snails that usurp the bulk of my time for empirical research. Opus 200 shall discuss the theoretical idea most central to my work—punctuated equilibrium. Moreover, Niles Eldredge and I formulated the theory of punctuated equilibrium in 1971, and I can scarcely resist the double whammy of 200 essays on the twentieth anniversary of "punk eke," the affectionate nickname used by supporters, while detractors have parried with "evolution by jerks."

Punctuated equilibrium began, as so much else that later looms large in our lives, as a little path that might never have opened. Paleontology, as the study of life's history, should be a jewel among the geological sciences; what subject could be more fascinating? Yet, until recently, it languished with an unjust reputation as a dull exercise in descriptive cataloging. Paleontologists were stereotyped as narrow specialists in mind-numbing particulars of favorite groups, places, and times. *Nature*, the British professional journal of science, editorialized about us in 1969:

Scientists in general might be excused for assuming that most geologists are paleontologists and most paleontologists have staked out a square mile as their life's work. A revamping of the geologist's image is badly needed.

During the 1960s, tumultuous for other reasons, a group of young paleontologists (including Eldredge and myself, then in that blessed stage of ontogeny) worked hard to reverse this image and to recapture the high reputation merited by more than 3 billion years of evolution. We felt that evolutionary theory provided the context for such a revitalization, and that the exclusively geological training then so traditional for paleontologists had fostered a reputation for dullness by excising the intellectual heart of the subject and leaving only the descriptive task of identifying fossils to tell the age of rocks and the environments of their formation.

We pursued our studies in biology as well and tried to use the latest concepts of evolutionary theory as a new foundation for interpreting life's history. We called our study paleobiology and eventually founded a journal of the same name, intellectually vital (sometimes frenetically so) and even profitable since its initial year in 1975. As a prelude, the late Tom Schopf sponsored a symposium at the 1971 meeting of the Geological Society of America in Washington, D.C.—Models in Paleobiology (published as a book in 1972).

Tom gathered all the young Turks and asked us each to apply a subject of evolutionary theory to the fossil record. He assigned me "speciation." I replied that I didn't know anything useful about speciation and would rather do "morphology" or "rates of change." He told me that he had already assigned these topics and that I had better "proceed" (euphemism) with speciation "or get off the pot." (I loved Tom, but he had a peremptory streak.) So I was stuck with speciation.

I wracked my brains, and my thoughts wandered back to graduate school, six years earlier, at the American Museum of Natural History (nose to the grindstone, but at least you could read this magazine for free each month). Niles Eldredge and I, as fellow students, had talked endlessly about potential reforms that a proper integration of evolutionary theory could bring to paleontology. Our most promising insight centered upon speciation, the origin of new and distinct biological populations. The prevailing opinion of paleontologists was mired in the deepest bias of Darwin's world view. Darwin, following Lyell's lead in geology, preferred to interpret substantial change as the insensibly gradual, incremental building of adaptation, tiny piece by tiny piece, generation by generation. Darwin used a striking metaphor to express his conviction that results of vast scale arise from minor inputs summed over geological immensity; the hero of evolution is time.

Natural selection is daily and hourly scrutinizing, 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….We see nothing of these slow changes in progress until the hand of time has marked the long lapse of ages [*Origin of Species*, 1859].

Beguiled by this vision, most paleontologists envisioned new species as arising by the insensibly slow and steady change of entire populations over long stretches of time, even by geological standards—a notion known as gradualism. Under this model, "*the* species problem in paleontology"—I put the phrase in quotes because it then resounded through our literature as a catechism—centered upon the difficulty of stating where ancestral species A ended and descendant species B began in such a continuously graded transition (the problem, so formulated, has no objective answer, only an arbitrary one).

And yet, while thus stating the issue in general writings, all paleontologists knew that the practical world of fossil collecting rarely imposed such a dilemma. The oldest truth of paleontology proclaimed that the vast majority of species appear fully formed in the fossil record and do not change substantially during the long period of their later existence (average durations for marine invertebrate species may be as high as 5 to 10 million years). In other words, geologically abrupt appearance followed by subsequent stability.

But how could traditional paleontology live with such a striking discordance between a theoretical expectation of gradual transition and the practical knowledge of stability and geologically abrupt appearance as the recorded history of most species? Our colleagues resolved their schizophrenia by taking refuge in a traditional argument, advanced with special ardor by Darwin himself—the gross imperfection of the fossil record. If true history is continuous and gradational, but only one step in a thousand is preserved as geological evidence, then a truly gradual sequence becomes a series of abrupt transitions. Darwin staked his whole argument on this proposition:

The geological record [is] extremely imperfect, and will to a large extent explain why we do not find interminable varieties, connecting together all the extinct and existing forms of life by the finest graduated steps. He who rejects these views on the nature of the geological record, will rightly reject my whole theory [*Origin of Species*, 1859].

This resolution worked in some logical sense, but it filled Niles and me with frustration and sadness. We were young, ambitious, enthusiastic, and in love with our subject. We had trained ourselves in evolutionary theory, particularly in the application of statistical methods to the measurement of evolutionary change, and we longed to get our hands dirty with practical applications. Our colleagues had virtually defined evolution as gradual change and had then eviscerated the subject as a paleontological topic by citing the imperfection of the fossil record to explain why we never (or so very rarely) saw direct evidence for the process that supposedly made life's history. This argument did resolve a contradiction (theoretical gradualism with overt punctuation), but at a crushing price for any practicing scientist, for if evolution meant gradual change, we could not discern the very phenomenon we most wished to study.

If this argument were sound, then so be it. Catch-22 rears its ugly head in many variations; sometimes you have to admit the intractable and move on to something else. But Niles and I realized that our evolutionary training, then rare for paleontologists, suggested an alternative reading full of fascination for its theoretical implications and promising as an honorable exit from the chill that Darwin's "argument from imperfection" had imposed upon evolutionary studies in the fossil record. (Before I forget, let me record that the ideas came mostly from Niles, with yours truly acting as a sounding board and eventual scribe. I coined the term *punctuated equilibrium* and wrote most of our 1972 paper, but Niles is the proper first author in our pairing of Eldredge and Gould.)

The idea that we eventually called punctuated equilibrium had two sources and one overriding purpose—to provide an exit from the "disabling rescue" of Darwin's argument on imperfection. First, a statement about mode of change: Most new species do not arise by transformation of entire ancestral populations but by the splitting (branching) of a lineage into two populations. Niles and I had learned the standard evolutionary version of speciation by branching—a notion popularized by Ernst Mayr and called by him the allopatric theory. *Allopatric* means "in another place," and the theory argues that new species may arise when a small population becomes isolated at the periphery of the parental geographic range. Isolation can occur by a variety of geological and geographic contingencies—mountains rising, rivers changing course, islands forming. Without geographic isolation, favorable variants will not accumulate in local populations, for breeding with parental forms is a remarkably efficient way to blur and dilute any change that might otherwise become substantial enough to constitute a new species. Most peripherally isolated populations never become new species; they die out or rejoin the larger parental mass. But as species may have no other common means of origin, even a tiny fraction of isolated populations provide more than enough "raw material" for the genesis of evolutionary novelty.

Second, a statement about rate of change. The simple claim that species arise by splitting, and not by transformation of entire ancestral populations, does not guarantee punctuated equilibrium. Suppose that most splitting events divide large populations into two units of roughly equal size, which then change at the conventional gradualistic rate. Splitting events, in this scenario, would yield two examples of gradualism—and the case for punctuated equilibrium would be compromised, not strengthened. Punctuated equilibrium gains its rationale from the ideal also a standard component of the allopatric speciation theory, that most peripherally isolated populations are relatively small and undergo their characteristic changes at a rate that translates into geological time as an instant.

For a variety of reasons, small isolated populations have unusual potential for effective change: for example, favorable genes can quickly spread throughout the population, while the interaction of random change (rarely important in large populations) with natural selection provides another effective pathway for substantial evolution. Even with these possibilities for accelerated change, the formation of a new species from a peripherally isolated population would be glacially slow by the usual standard of our lifetimes. Suppose the process took five to ten thousand years. We might stand in the midst of this peripheral isolate for all our earthly days and see nothing in the way of major change.

But now we come to the nub of punctuated equilibrium. Five to ten thousand years may be an eternity in human time, but such an interval represents an earthly instant in almost any geological situation—a single bedding plane (not a gradual sequence through meters of strata). Moreover, peripheral isolates are small in geographic extent and not located in the larger area where parents are living, dying, and contributing their skeletons to the fossil record.

What then is the expected geological expression of speciation in a peripherally isolated population? The answer is, and must be, punctuated equilibrium. The speciation event occurs in a geological instant and in a region of limited extent at some distance from the parental population. In other words, punctuated equilibrium—and not gradualism—is the expected geological translation for the standard account of speciation in evolutionary theory. Species arise in a geological moment—the punctuation (slow by our standards, abrupt by the planet's). They then persist as large and stable populations on substantial geological watches, usually changing little (if at all) and in an aimless fashion about an unaltered average—the equilibrium.

Most of our paleontological colleagues missed this insight because they had not studied evolutionary theory and either did not know about allopatric speciation or had not considered its translation to geological time. Our evolutionary colleagues also failed to grasp the implication, primarily because they did not think at geological scales. But whatever the theoretical meaning of punctuated equilibrium, Niles and I were most pleased by its practical and heuristic value. We had reinterpreted the fossil record as an accurate reflection of evolution, rather than an embarrassment that made reality (read gradualism) invisible by its imperfections. We gave paleontologists something to do, a way to get hands dirty. Evolution can be studied directly; change by the ordinary route of allopatric speciation is palpable in geological evidence. Stop apologizing for natural imperfections and get to work.

I showed our initial article to my father. He said, "This is terrific; it will really shake things up." I replied, "Nobody will read it, and no one will pay any attention." He was right. He usually was.

Punctuated equilibrium provoked a major brouhaha, still continuing, but now in much more productive directions. With my vicennial perspective, I can identify both bad and good in the extensive debate. Three points stand out on the negative side. First, simple misunderstanding of basic content was distressingly common, even among professional evolutionists. Many colleagues thought that we had raised the old anti-Darwinian specter of macromutationism, or truly sudden speciation in a single generation by a large and incredibly lucky mutation. I do not know why this happened; I think that all our articles and public statements were clear in separating human from geological rapidity. The theory, after all, is rooted in this distinction—for punctuated equilibrium is the recognition that gradualism on our mortal measuring rod of three score years and ten translates to suddenness at the planet's temporal scale. Many less than adequate press reports conveyed this disabling confusion (others were very accurate). Some colleagues probably read no further. For others, the very word "sudden" raised such hackles that anger displaced critical thought, and they never probed the key distinction.

Second, the theory became an issue (quite coincidentally) just when creationism reached its acme of thankfully temporary influence. Creationists, with their usual skill in the art of phony rhetoric, cynically distorted punctuated equilibrium for their own ends, claiming that we had virtually thrown in the towel and admitted that the fossil record contains no intermediate forms. (Punctuated equilibrium, on the other hand, is a different theory of intermediacy for evolutionary trends—pushing a ball up an inclined plane for gradualism, climbing a staircase for punctuated equilibrium.) Some of our colleagues, in an all too common and literally perverse reaction, blamed us for this mayhem upon our theory. At least we were able to fight back effectively. Most of my testimony at the Arkansas creationism trial in 1980 centered upon the creationists' distortion of punctuated equilibrium.

Third, and this is harder to say but cannot be ignored, a few colleagues allowed personal jealousy to cloud their judgment—for their vitriol simply cannot be understood as a response to intellectual issues. Punctuated equilibrium got a good dollop of publicity—including editorials in the *Times* of India and articles in the Beijing *People's Daily*. Some colleagues assumed that we had orchestrated all this with the help of press agents and largely for personal glory. Why not consider the more honorable altemative—that we had raised interesting and important issues, and that people (as basically intelligent entities) responded?

But the good has far outweighed these frustrations. No scholar can ask for more than a serious consideration of his ideas, and no scientist can hope for more than the conversion of his concepts into fruitful research (whatever the fate of particular nuances and centralities). The great joy of punctuated equilibrium has been its extension (largely by others) into areas and implications that we never even conceptualized at the inception. I cringe now when I read our original paper of 1972. Both sides of the theory have been useful to our profession.

On stasis (equilibrium). Niles and I, with some grammatical (but no intellectual) doubt, soon took as the motto of punctuated equilibrium: "Stasis is data." We see the world in the light of theories and ideas; as Peter Medawar said, "Innocent, unbiased observation is a myth." My greatest pride in punctuated equilibrium lies in its role in turning the basic fact of paleontology from an unstated embarrassment into a subject of active and burgeoning research. When most of our colleagues defined evolution as gradual change, the stability of species counted as no data—that is, as absence of evolution. All paleontologists recognized the stability of species, but the subject never entered active research. At most, the fact of stability might be noted in the midst of a taxonomic description. Punctuated equilibrium has changed the context. Stasis has become interesting as a central prediction of our theory. No one, twenty years ago, would have dreamed of publishing a paper about the lack of change in some particular brachiopod during umpteen million years in Michigan. But is it not intrinsically fascinating, in a world of change and a history of life crafted by evolution, that species don't alter over such extended stretches of time? Don't we want to know why so many species *don't* change for so long? Stasis is a puzzle, not a negativity. Paleontologists now routinely document stasis; many studies are complexly quantitative and meticulously elegant. I am proud that punctuated equilibrium served as the midwife for this fruitful work.

Moreover, given the invisibility of stasis in older paleontological literature, many students of modern organisms simply didn't know about this primary fact of the fossil record; they assumed that gradual change was the norm for most species most of the time. Stasis is now generally recognized as an intriguing puzzle by evolutionists. No definitive resolution is in sight, but geneticists and embryologists have offered their counsel, and I am tickled that our much maligned profession (dull, descriptive paleontology) has provided such a puzzle to kings of the theoretical mountain.

On punctuation. Punctuated equilibrium has provided a new context for the most important phenomenon of paleontology—evolutionary trends (larger size in horses, more complex sutures in ammonites, bigger brains in humans). Under gradualism, trends arise because natural selection favors some traits over others, and a genealogical continuum builds these features further and further along the path of advantage. Species are arbitrary segments of the resulting continuum—a largely artificial consequence of change. Punctuated equilibrium cleanly reverses this perspective. Species are real units, arising by branching in the first moments of a long and stable existence. A trend arises by the differential success of certain kinds of species. (if large-bodied horses either arise more frequently or live longer than small-bodied horses, then a trend to increased size will permeate the equine bush.) Speciation is the real cause of change, not an arbitrary consequence of artificial division of a continuum. Since the causes of branching are so different from those of continuous transformation, trends must receive a new explanatory apparatus under punctuated equilibrium.

Enough puffery for consequences of the theory. What about a more basic question? Is punctuated equilibrium true? I suppose I'm the worst person to ask. What parent would hand his child to the executioner, whatever the kid's shortcomings? Nature is a domain of relative frequencies, not absolutes. Niles and I never denied that cases of gradualism would be found, just as the most ardent Darwinian selectionist does not claim exclusivity for his favored mechanism of change, but only a presence overwhelming enough to shape the major patterns of life's history. On this proper ground, I am confident that punctuated equilibrium does prevail as the primary molder of pattern in the fossil record. Others would disagree on the totality, but all would concur that punctuated equilibrium is a real and important phenomenon, and that many elegant studies of its operation have been published in the past two decades—Cheetham on bryozoans, Ager on brachiopods, Stanley and Yang on clams, Williamson on snails, Prothero and Shubin on horses, to name just a few. The current "out of Africa" versus "candelabra" debate on human evolution represents a claim for speciation and punctuated equilibrium in our own origin.

But my greatest pleasure has been the passage of punctuated equilibrium from a much debated theory to an ordinary instrument of active research. To cite just one example, a prominent criticism of punctuated equilibrium has held that the morphologically stable "entities" documented in the fossil record might not be true biological species by the proper definition of a population reproductively isolated from all others (breeding only among its members and not with others—a criterion of ultimate and permanent evolutionary independence). Perhaps, the critics say, many of these morphological "packages" hide several species of virtually identical body form, but differing in properties not preserved in the fossil record (color, behavior, and so on). Such so-called cryptic species are quite common in some groups. On the other hand, some packages might be only parts of highly variable species, with other geographically distant populations as portions of the same unit by proper reproductive criteria.

The best treatment of this objection must be sought in studies of living species with good fossil records—where direct surveys can be made for correspondence of a morphological package with a true biological species, and the origin and history of the same package can then be traced in the fossil record and assessed for punctuated equilibrium. I am delighted to report that two such pioneering studies have been published in the past few years, and both support punctuated equilibrium.

New Zealand biologist B. Michaux did a morphological and genetic survey of four species in the snail genus *Amalda*. He found no cryptic populations; each morphologically defined package corresponds perfectly with a biological species. Three of these species extend back in the New Zealand fossil record for several million years. In an elegant, multivariate study of morphological pattern, Michaux demonstrated stasis throughout the ranges of all species. He concludes (in the *Biological Journal of the Linnaean Society of London*, vol. 38, 1989):

This study demonstrates that fossil members of three biologically distinct species fall within the range of variation that is exhibited by extant members of these species. The phenotypic trajectory of each species is shown to oscillate around the modern mean through the time period under consideration. This pattern demonstrates oscillatory change in phenotype [our jargon for overt morphological appearance as contrasted with underlying genetics, or genotype] within prescribed limits, that is, phenotypic stasis.

In a second study (*Science*, vol. 248, 1990), Jeremy Jackson and Alan Cheetham studied eight species in three genera of bryozoans. These colonial marine organisms are so highly variable, and supposedly so subject to immediate shaping by nongenetic forces (temperature, crowding, and so on), that many biologists have doubted any correspondence between morphological package and true biological species and have even doubted that morphological packages could be specified at all. But Jackson and Cheetham, in a series of carefully controlled experiments, first determined that they could find no cryptic species within any of the packages (coincidence of morphological and biological species). They then grew two generations of the species in a common environment to see if the morphological distinctions were truly inherited or merely a transient result of growing in certain places under certain conditions. Each package checked out as genetically distinct and morphologically unique and stable. They conclude:

Our results show that the identity of quantitatively defined morphospecies of cheilostome bryozoans is both heritable and unambiguously distinct genetically. . . . Thus, cheilostome morphospecies appear to be good biological species.

Since Cheetham had presented the most elegant and persuasive of all cases of punctuated equilibrium in his studies of the cheilostome bryozoan Metrarabdotos (in *Paleobiology*, 1986 and 1987), these findings increase our confidence in his results. Jackson and Cheetham end their paper with these words:

The consistency of our results across three distantly related cheilostome genera suggests that previously documented patterns of morphologic stasis punctuated by relatively sudden appearances of new morphospecies in the cheilostome Metrarabdotos do indeed reflect patterns of evolution at the species level. This is consistent with the punctuated equilibrium model.

As ordinary human beings with egos and arrogances, scientists love to be right. But we would, I think, all say that to be useful is more important, that is, to propose an idea that gets people excited and suggests fruitful strategies for potential confirmation and disproof. The jury is still out on the relative frequency of punctuated equilibrium (twenty years is a short case in biology), but utility has already been proved in the pudding of practice.

On the subject of things that come in twenties and then lead on to greater fruitfulness, I can only quote some lines of Robert Herrick, with their delicious final rhyme:

Give'me a kiss, and to that kiss
  a score;
Then to that twenty, add
  a hundred more:
A thousand to the hundred:
  so kiss on,
To make that thousand up
  a million.

Now we're getting to proper geological scales!