

natural selection, are spelled out painstakingly throughout most of the book. Indeed, religious considerations led to suppression of his theory for about 20 years, but it becomes clear that other political and social factors played equally important roles in his decision to withhold publication until Alfred Wallace entered the scene.

The depth of this book is exemplified by the fact that one must read nearly 500 pages before encountering the famous denunciation of Bishop Wilberforce by Thomas Henry Huxley. Of course, Darwin was not there to hear it—he rarely attended such meetings, begging off most of the time because of chronic ill health that plagued him for most of his life. But he was pleased by Hooker's narrative of the proceedings which, like nearly everything else, he saved for posterity. And this one aspect of Darwin's personality, an almost pathological obsession with collecting, note-taking, and hoarding, is precisely what made this book possible. Not only did he save everything related to his research as a naturalist working with barnacles, pigeons, insectivorous plants, beetles, orchids, rabbits, and earthworms, he also listed and accounted for everything of a personal economic nature (e.g., expenditures for fat drippings) and even the regular backgammon matches with his wife, Emma:

"Emma, 'poor creature, has won only 2,490 games, whilst I have won, hurrah, hurrah, 2,795 games!'" (p. 619).

Without this penchant for meticulous observation, recording, and dissection, even to the point where Darwin himself often thought his work complete drudgery, he might very well have never arrived at the concept of evolution by natural selection and, in so doing, revolutionizing biological thought thereafter. This was all a part of his genius; the other was the ability to fit all the pieces together in a theoretical explanatory framework, which he did. One can only wonder about the result had he been aware of Gregor Mendel who, to paraphrase Dobzhansky, could have given him the genetic keystone to the arch he was building. But that was not to happen.

I thought that I knew a good deal about the life of Charles Darwin, having once taught a course on the history of evolutionary theory. But I really knew very little about the man until now, and sincere gratitude for expanding my knowledge goes to Desmond and Moore for this splendid work.

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THE DYNAMICS OF EVOLUTION: THE PUNCTUATED EQUILIBRIUM DEBATE IN THE SOCIAL AND NATURAL SCIENCES. Edited by Albert Somit and Steven A. Peterson. Ithaca, NY: Cornell University Press. 1992. vi + 325 pp. ISBN 0-8014-9763-9. \$47.50 (cloth). \$17.95 (paper).

Charles Darwin's natural selection is a theory that explains profound change in the history of life by differential conservation of minute differences distinguishing individuals of a species. Change itself is counterintuitive because it contradicts experience: no one has ever seen the origin of a species, and species change so little on the scale of a generation or two (the scale of our lives) that something special seems required to explain

the origin of new species. Evidence of profound change comes from the fossil record (which is as true today as it was in Darwin's time). The key to Darwin's theory is the long duration of geological time, permitting small differences to accumulate gradually, step-by-step, generation-by-generation, fast or slow, with the passage of many generations. Thus human children are closely similar to their parents, while differing conspicuously from *Homo erectus* and earlier ancestors.

Saltation and macromutation are biologists' names for special theories to explain the origin of new species in the absence of observable change in their ancestors, while quantum evolution and punctuated equilibrium are paleontologists' names for similar theories. The former reflect conviction that

species arise too rarely to study in the living present, and the latter reflect conviction that species arise too rapidly to study in the geological past. Personally, I think much of the problem comes from comparing evolutionary change on the scale of biological generations with change on the scale of geological ages—biologists rarely measure change with enough precision and consequently fail to see it, and paleontologists rarely sample time finely enough to detect intermediates and consequently think they do not exist.

The Dynamics of Evolution was organized and edited by two political scientists, Albert Somit and Steven Peterson, to clarify punctuated equilibrium and to explore its meaning for the social and behavioral sciences. Questions of interest included: How does change occur in the biological world? Does it happen gradually, as classical evolutionary theory long assumed, or does it occur by abrupt transformations of structure and behavior? Is the nature of biological change relevant for our understanding of human behavior and, if so, how? Ernst Mayr, Stephen Jay Gould, Steven Stanley, Niles Eldredge, Antoni Hoffman, and Michael Ruse were invited to clarify punctuated equilibrium, and Kenneth Boulding, Susan Cachel, Allen Mazur, Brian Gladue, Glendon Schubert, and Roger Masters were invited to discuss its implications for the behavioral sciences. Punctuated equilibrium must tell us something about change in animal evolution before it can have implications for human social and behavioral change, and I will concentrate on the punctuated equilibrium chapters here.

Ernst Mayr opens the book with a chapter on “speciational evolution,” considered the core of punctuated equilibrium theory, which he developed and published in 1954 and again in 1963. Mayr claims that the most rapid evolutionary change occurs during cladogenesis (the only kind of speciation to Mayr and some other biologists) in small peripatric founder populations (p. 25), an idea he developed studying speciation in New Guinea birds. Mayr asks, “Does peripatric speciation speed up evolution?” and candidly answers, “Honesty demands that we admit a lack of concrete knowledge that would permit us to answer [this] question.

All that we can do at present is to hypothesize; and in that respect we have not made much progress since 1954” (p. 37).

Mayr considers the core ideas of punctuated equilibrium to be 1) most or all change occurs during speciation [cladogenesis] events, and 2) most species usually enter a phase of total stasis after the end of the speciation process. He writes: “A modest theory of punctuationism is so strongly supported by facts, and fits, on the whole, so well into the conceptual framework of Darwinism, that one is rather surprised at the hostility with which it was attacked” (p. 27). Mayr also writes that “all population evolution—that is, all evolution we are concerned with—is gradual” (p. 37). If punctuationism was vigorously challenged, it might be because Eldredge and Gould emphatically claimed it was an *alternative* to gradualism. At a deeper level, it might also be because Mayr’s oft-cited ideas of “internal cohesion of the genotype” protected by “intrinsic barriers to reproduction” are now in question. Mayr writes that “thawing out of the congealed part of the genotype” (p. 43) is possible in founder populations—what can this mean (and what does it mean for speciation)? Mayr’s characterization of paleontologists as typologists adopting “sympatric saltational speciation” (p. 23) and his dismissal of geneticists as reductionists (p. 34) are surprising for a contemporary of G.G. Simpson, T. Dobzhansky, and other co-architects of the modern evolutionary synthesis.

Gould describes punctuated equilibrium as 1) a testable theory about the origin of species and their geological deployment, 2) a theory based on recognition that events slow in ecological time might appear instantaneous in geological resolution, and 3) an idea resolvable within the rubric of known mechanisms and causes (p. 57). It is a theory of alternating rapid change and stasis. Gould writes that “most punctuations are lost in imperfections of the fossil record” (p. 63), while stasis means “a species looks at its end as it did at its beginning” (pp. 63–64). These characterizations are too vague to make the theory testable. What do “slow in ecological time” and “instantaneous in geological resolution” mean? Why can’t anything be quantified?

Gould does not like extrinsic stabilizing selection as an explanation for stasis, because stabilizing selection acts “here and now,” while “geological stasis lasts for millions of years.” Rather, he writes, “the profoundness and temporal depth of stasis are trying to tell us that change is *actively prevented* . . . by evolved genetic and developmental coherences” (p. 64, italics in original). This sounds like more of Mayr’s “internal cohesion of the genotype,” and is hardly part of the rubric of known mechanisms and causes. Whatever the explanation for stasis, stasis does not distinguish punctuated equilibrium from Darwin’s gradualism. Gould argues again that gradualism is about rates, which it is not, etymologically or by any definition in my dictionary (p. 71). Hoffman clarifies this, indicating that Eldredge and Gould [mis]understand gradualism to be orthogenesis—unidirectional evolution at a constant rate caused by orthoselection in an entire species (p. 124).

Cachel reviews punctuated equilibrium from the point of view of evolutionary anthropology, finding that “the appearance of dogmatic cladistic systematics, . . . denigration of adaptation or natural selection, [and] return to typology . . . reflect the influence of punctuated equilibrium theory” (p. 194). I don’t know if all can be blamed on punctuated equilibrium per se, but these do seem related in some way.

Gould and others write as if punctuated equilibrium is all paleontologists have to contribute to the understanding of evolution, which is nonsense. There is much to learn about the scaling of patterns and rates of change from fossils. The fossil record shows that evolutionary history is punctuated on the scale of geological stages and ages, but there is every reason to think this correlates with global events of environmental change, and no reason to imagine that it has anything to do with peripatric speciation on a completely different time scale. Similarly, species “sorting” and other hierarchical aspects of macroevolution do not depend in any way on peripatric speciation.

Punctuated equilibrium was born in the

early 1970s. For me, it died then too, because punctuation and stasis do not describe the patterns of change anyone can quantify in *Plesiadapis*, *Hyopsodus*, *Cantius*, and a host of other complex Cenozoic mammals with well-sampled fossil records. Punctuated equilibrium is a view of evolution one gets studying “living fossils” and long-lived invertebrates so simple they “generally . . . are not observed to vary” (fide Eldredge, p. 106), let alone change. Maybe paleontologists *are* saltational typologists! We may now know the distribution of durations for all species, but we do know living fossils are extremes drawn from one tail and cannot be representative.

Advocating that most change is lost in events we cannot see or study is another way of arguing that much of the fossil record is poor, but why base a whole punctuated equilibrium theory of evolution on the part that is poor? The fossil samples I am familiar with show population variation when studied quantitatively—and these, like living populations, show change when studied through time. Species that do not appear to change may be in dynamic equilibrium, but this “stasis” too is easily explained by selection—it requires neither “internal cohesion of the genotype” nor “evolved genetic coherences.” Natural selection is a simple, elegant, powerful stochastic explanation for change that anyone with the slightest understanding of variation and statistics can appreciate.

As editors, Somit and Peterson have produced a fine book that should be read carefully by anyone still interested in punctuated equilibrium. The contradictions and inconsistencies are all reviewed (and many are repeated). Somit and Peterson were surprised by the range and depth of disagreement concerning punctuated equilibrium after 20 years of debate. I am, too. Simpson himself gracefully buried quantum evolution after a decent interval of only 9 years.

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