



## **Punctuated Equilibrium and the Fossil Record**

Thomas J. M. Schopf; Antoni Hoffman; Stephen Jay Gould

*Science*, New Series, Vol. 219, No. 4584 (Feb. 4, 1983), 438-440.

Stable URL:

<http://links.jstor.org/sici?sici=0036-8075%2819830204%293%3A219%3A4584%3C438%3APEATFR%3E2.0.CO%3B2-6>

*Science* is currently published by American Association for the Advancement of Science.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/aaas.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

## LETTERS

### Punctuated Equilibrium and the Fossil Record

In seeking to go beyond Darwinism and its view of the evolution of life, Stephen Jay Gould asks (23 April, p. 380), "What would a fully elaborated, hierarchically based evolutionary theory be called?" In 1980, Gould wrote to aid his view of hierarchy by providing names to rungs on the ladder [Goldschmidt break between adaptation in local populations and speciation and Wright break between speciation and macroevolutionary trends (1)]. Thus by providing both structure and names to phenomena, he has provided a subject that can be talked and written about.

But, one should ask, is a static hierarchy a true and correct view of life? Gould supports his views by writing (omitting his caveats), "Is our world . . . primarily one of constant change (with structure as a mere incarnation of the moment), or is structure primary and constraining, with change as a 'difficult' phenomenon, usually accomplished rapidly when a stable structure is stressed beyond its buffering capacity to resist and absorb." He votes for stability of biological species, with continual change "difficult."

As a core assertion in his evolutionary view, Gould writes that "punctuated equilibrium" prevails and that stasis is common, ". . . as paleontological experience affirms (overwhelmingly for marine invertebrates, at least)." However, to the best of our knowledge, punctuated equilibrium, with stasis at its core, is not widely accepted within the paleontological profession in either America or Europe. Indeed, few generalizations one could make about biological species and the fossil record are more in question than either punctuated equilibrium or stasis.

Among the fossils on which the assertion of stasis historically is based are the garden-variety larger invertebrates—the brachiopods, trilobites, bivalves, snails, and corals. For these organisms, population samples are not available every few centimeters over a stratigraphic section representing continuous sedimentation for several million years, nor is there fully acceptable geographic control. Usable specimens of most species occur sporadically, and data are routinely combined from an outcrop, or several outcrops, either in the field or later in the laboratory; material is then said to characterize a given formation (2). Such collections are made to correlate forma-

tions (not to document evolutionary patterns). By this procedure, possibilities for recognizing change are lumped together by the sampling process; in most cases the shortest time interval one can say anything about would be the duration of a particular geologic formation (a value that is on the order of  $10^5$  to  $10^6$  years).

Records on duration of species and genera are not summarized by formation but by the yet more inclusive unit, the geologic stage (3). For example, data on generic durations in the more than 30 volumes of the *Treatise on Invertebrate Paleontology* are given to geologic stage. It is difficult to estimate stage durations, let alone try to estimate the shorter, and often time-transgressive, formation durations. In most circumstances the minimum species or generic duration becomes approximately the mean duration of a geologic stage (a few to several million years) (3, 4). The appearance of stasis inevitably would result from the way the data are sequentially grouped together. Rarely, if ever, are durations of species for any major group of organisms for any considerable part of geologic time based on the actual distribution of specimens in the rock record.

Even if larger invertebrates could be collected on a bed-by-bed basis, at least three other biases of great significance act artificially to lengthen durations of recorded "species" (5). However, if one were able to take all four biases into account, one still could not make a firm decision about the mode of evolution. When Raup and Crick (6) evaluated the paleontologically excellent data set of Brinkmann on the paleontologically famous Jurassic ammonite *Kosmoceras*, the trends in morphology showed gradualistic changes by any reasonable morphologic definition of gradualism. Yet Raup and Crick concluded that it was impossible to arrive at a decision about punctuated equilibrium versus gradualism because one could not determine if one were dealing with biological species. In other words, depending on one's opinion of a biological species, one could answer the question of the mode of evolution any way one wanted.

What about testing the theory with paleontological material that is more suitable than the larger marine invertebrates? In some instances, one can obtain hundreds of specimens of "species" of microfossils on a centimeter-by-centimeter basis for several million years. Detailed studies (7) were carried out [akin to the *Kosmoceras* study by Raup and Crick (6)], and the authors concluded that gradualism is without question

the mode of evolution. Further, studies of fossil mammals (8), including a statistical comparison with a null hypothesis of punctuated change, also revealed that gradualism prevailed in a majority of instances. Hominid evolution, once considered a prime example of punctuated equilibrium, owing (we think) to the paucity of fossil specimens, after the analysis of additional material has been tied to gradualistic change (9). In these examples from microfossils (foraminifera, Radiolaria, and conodonts) and from mammals, one may not be dealing with biological species any more than, say, in the case of the ammonite *Kosmoceras*. But when the conditions of sampling and statistical analysis have been rigorously developed, paleontologists of different backgrounds, working with organisms of different geologic ages, have found (6–9) gradualism to be a sensible interpretation of most of the data.

One could say that, if biological species cannot be determined, then trends in particular "morphological" characters should be examined. That is fine. But, if so, one is no longer referring to a theory about biological species, which was the focus of punctuated equilibrium. The problem of the origin and duration of species is not the same as the problem of stability in form of morphological "hard parts" over geologic history (10, 11). This is why even such data as the mean duration of several bivalve morphospecies of close to 20 millions years (12) cannot provide evidence for stasis of biological species.

Once punctuated equilibrium is seen as a hypothesis that is virtually impossible to test (at least in the fossil record) and highly questionable on biological grounds (13), there is no reason to postulate macroevolutionary mechanisms ("species selection," for example) to account for evolutionary trends.

The questioning of the empirical support for punctuated equilibrium also undermines Gould's view of species as individuals (that is, as essences) and the far-reaching consequences of that philosophical view. This use of "species as individuals" does not appear to be what Hull (14), at least, had in mind. We doubt that species can justifiably be considered as biologically discrete in time, and thus they should not be treated as individuals for biological purposes. If they are not, then species as individuals cannot interact with other species as individuals, as in the customary species selection model. Convincing evidence for the efficacy of "species selection" is lacking, and Gould himself writes that "sorting out among higher-level individuals may arise

solely from natural selection operating upon organisms.”

When one evaluates the inherent biases of the fossil record and includes relevant information from genetics and molecular biology (15), the outstanding feature of species evolution is not stasis, but change; and species selection, which Gould (16) calls “the strongest argument for macroevolution,” becomes unacceptable.

THOMAS J. M. SCHOPF

Department of the Geophysical  
Sciences and Committee on  
Evolutionary Biology, University of  
Chicago, Chicago, Illinois 60637

ANTONI HOFFMAN

Institut für Geologie und Paläontologie,  
Universität Tübingen,  
D-7400 Tübingen 1, West Germany

#### References and Notes

1. S. J. Gould, *Paleobiology* 6, 119 (1980).
  2. A formation is a technical geological term that customarily refers to a lithologic unit of sufficient dimension that it can be represented on standard scale geological maps. Formations typically are from several meters to tens or hundreds of meters in thickness.
  3. A stage is a technical geological term for a time interval that typically includes a succession of biostratigraphic zones. The mean duration of a Phanerozoic stage is about 8 million years. Stages are usually the first subdivision for which it is practical to correlate on a worldwide basis. For durations, see J. J. Sepkoski, Jr., *Paleobiology* 1, 343 (1975).
  4. Some authors have sought to take into account the fact that (on a probabilistic basis) a taxon will not occur throughout the full subdivision of geologic time to which it has been assigned. However, these corrections are not based on actual detailed records of taxa, and the number to be corrected is always the longer time interval to which the fossil was initially assigned. A cohort method of estimating durations was recently introduced [D. M. Raup, *Paleobiology* 4, 1 (1978)]. However, the first census point for each of the geologic system generic cohorts is after 90 percent of each cohort is no longer existing. Species durations were obtained in a backward calculation from inferred generic survivorship. This is not (nor was it represented to be) a direct measure of species durations.
  5. These include (i) the effects of including the very large number of taxa with few morphological features and for which evolutionary change cannot be adequately assessed; (ii) the unavoidable effects of basing mean durations on the most common (that is, most widespread “species” with seemingly the longest durations), whereas if full collecting were carried out most species would be rare and of short duration; and (iii) the sheer necessity to lump within one morphological form species distinguished by diagnostic hard parts that are not preserved, soft parts, and all sibling species (which at any given moment in time, if the present is any guide, may account for 10 to 20 percent of the species of many major groups). These biases have been estimated to lengthen species durations by a factor of 10 to 100. Instead of mean durations of species being, say, 5 million years, they are more likely 50,000 to 500,000 years (on the order of  $10^5$  years instead of  $10^7$  years). These revised durations do not represent stasis [T. J. M. Schopf, *Evolution* 36, 1144 (1982)].
- Opposed to the above, the chief argument in favor of lengthening ranges is that the fossil record is always incomplete, and hence ranges are truncated. That argument loses force to the extent that biological species are anticipated to have short ranges. The best estimates of mean species durations from fossils are likely to be from species that appear to be evolving the most rapidly [T. J. M. Schopf, *Paleobiology* 7, 156 (1981); (15)]. If so, then the chief effect of having an incomplete fossil record is in the sheer absence of most species and not in the lengthening of ranges of those species that do occur, given

- all of the biases that automatically artificially serve to increase their ranges.
6. D. M. Raup and R. E. Crick, *Paleobiology* 7, 200 (1981).
  7. B. A. Malmgren and J. P. Kennett, *ibid.*, p. 230; D. B. Lazarus, J. D. Hays, D. R. Prothero, *Third North Am. Paleontol. Conv. Proc.* (1982), vol. 1, p. 323; J. Dzik and J. Trammer, *Acta Palaeontol. Pol.* 25, 55 (1980).
  8. F. L. Bookstein, P. D. Gingerich, A. G. Kluge, *Paleobiology* 4, 120 (1978).
  9. J. E. Cronin, N. T. Boaz, C. B. Stringer, Y. Rak, *Nature (London)* 292, 113 (1981).
  10. A. Hoffman, in *Concept and Method in Paleontology, Contributed Papers*, J. Martinell, Ed. (University of Barcelona, Barcelona, 1981), pp. 57–63; *Evol. Biol.* 15, in press.
  11. T. J. M. Schopf, *Paleobiology* 7, 156 (1981).
  12. A. Hoffman and B. Szubzda-Studencka, *Neues Jahrb. Geol. Palaeontol. Abh.* 163, 122 (1982).
  13. See B. Charlesworth *et al.*, *Evolution* 36, 474 (1982); C. A. Lemen and P. W. Freeman, *Paleobiology* 7, 311 (1981); M. E. Douglas and J. C. Avise, *Evolution* 36, 224 (1982).
  14. D. L. Hull, *Annu. Rev. Ecol. Syst.* 11, 311 (1980).
  15. T. J. M. Schopf, in *Paleobotany, Paleoeology, and Evolution (Festschrift for H. P. Banks)*, K. J. Niklas, Ed. (Praeger, New York, 1981), vol. 1, pp. 135–192.
  16. S. J. Gould, in *Perspectives on Evolution*, R. Milkman, Ed. (Sinauer, Sunderland, Mass., 1982), pp. 83–104.

Schopf and Hoffman present once again their well-known and oft-expressed criticisms of punctuated equilibrium (1). My article in *Science*, however, was not a defense of punctuated equilibrium but an argument for expanding Darwinian styles of explanation to a hierarchy of biological levels, particularly to the species as a unit of selection. Punctuated equilibrium, to be sure, aids this argument substantially, since species are better individuated if they do not change during their lifetimes. But punctuated equilibrium is not a prerequisite for species selection, since stability is not a criterion for designating individuals. Organisms have ontogenies with substantial change, as Oedipus informed the Sphinx, yet they remain our quintessential individuals. The proper prerequisite holds that most evolutionary change arises with the production of new species (individuals) by branching and not by the transformation of lineages without branching. Species may certainly change (as organisms do), provided that evolution is not primarily the story of their transformation in toto into other individuals (as organisms do not).

Nonetheless, since they brought it up, Schopf and Hoffman’s critique of punctuated equilibrium is rooted in a misunderstanding about the database of this theory. The fundamental claims—geologically abrupt appearance of new species and stasis within established species—were not “discovered” by Eldredge and myself (2) but represent the basic observation of field-oriented paleontologists who have studied “garden-variety larger invertebrates” since Cuvier’s time (3). Darwin (4) and all the great gradualists did not deny this pattern but attempted to explain it as the

artifact of an imperfect record—or, rather, they subtly ignored stasis as “no data” and attributed abrupt appearance to imperfections. Eldredge and I argued that this standard pattern need not be seen as an artifact but may represent the proper scaling into geological time of the ordinary process of speciation as understood by modern biologists—abrupt appearance as the normal duration of speciation in small, isolated populations (thousands of years) when expressed in the geological record, and stasis as the expected pattern in large, successful, central populations.

Thus, stasis cannot be an artifact of how the *Treatise on Invertebrate Paleontology* compiles (or compresses) data, since the pattern was not discovered by epistemic theorists working with books but represents the standard field experience of conventional empiricists who study long sections in situ and do not merely compile disparate data from separated places (as Schopf and Hoffman charge). Consider just one testimony from a lifetime of experience (5):

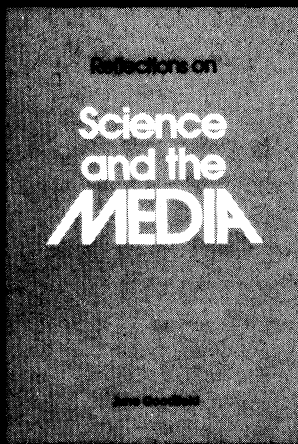
During my work as an oil paleontologist I had the opportunity to study sections meeting these rigid requirements [long, well-represented sequences]. As an ardent student of evolution, moreover, I was continually on the watch for evidence of evolutionary change . . . The great majority of species do not show any appreciable evolutionary change at all. These species appear in the section (first occurrence) without obvious ancestors in underlying beds, [and] are stable once established . . .

Since Eldredge and I advanced punctuated equilibrium, many excellent documentations of stasis have been published (6, 7), but Schopf and Hoffman cite not a single one. (Eldredge and I emphasized stasis because it is not so subject to imperfections of the record and is therefore far easier to test than our other cardinal phenomenon of geologically abrupt appearance. Yet even abrupt appearance has been resolved to punctuation rather than imperfection in an exceptionally favorable set of cases (7), again not mentioned by Schopf and Hoffman). These examples of stasis either involve single long and well-sampled sections (therefore not subject to the criticisms of Schopf and Hoffman about amalgamation and summarization of data) or represent accumulated empirical experience in detailed local collecting with adequate geographic control (equally not subject to artifacts of sequential grouping).

As a second criticism, Schopf and Hoffman admit to some morphological stasis but argue that limitations of pale-

## ARE THE MEDIA FAIR TO SCIENCE? IS SCIENCE FAIR TO THE MEDIA?

Read *Reflections on Science and the Media*, a provocative new book by June Goodfield, author of *An Imagined World*, and decide for yourself.



"If any slim volume can help combat the polarisation which so easily afflicts discussion of media science, this is it. Apart from being limpidly written, the book succeeds well because it returns constantly to the machinery and manpower of the media."

—Bernard Dixon, *New Scientist*

128 pp. 1981  
ISBN: 0-87168-252-4  
Paper, \$9.00  
AAAS member price, \$8.00

Mail order to:  
AAAS Sales Dept. SM3V  
1515 Massachusetts Ave., NW  
Washington, DC 20005

Please allow 6-8 weeks for delivery.  
All orders under \$10.00 must be prepaid.

ontological data preclude any adequate analysis of species. This old dilemma did not arise with punctuated equilibrium; it forms the classic "species problem in paleontology" (8). Most paleontologists admit these limits in most cases but point to the number of favorable examples where geographic control and, particularly, the sympatric occurrence of forms with their ancestors or sister taxa provide as much evidence as neontologists generally obtain in designating species. As a related point, Schopf and Hoffman argue that systematic biases greatly overestimate the ranges of fossil species. While I disagree strongly and suspect that, if anything, the longevity of most fossil species may be underestimated by actual occurrences (9), I fail to see the relevance of this point to the validity of punctuated equilibrium. The issue is whether or not most species are stable after their origin, not how long they last. Indeed, shorter durations and more species would be favorable for the most important implication of punctuated equilibrium and another phenomenon denied by Schopf and Hoffman—species selection (since any Darwinian process of selection requires copious raw material, and species themselves are raw material at this hierarchical level).

As their third criticism, Schopf and Hoffman charge that punctuated equilibrium is untestable. Yet many tests have been made, for better or for worse [several good cases of gradualism have been documented, including, in my opinion, that of Raup and Crick on *Kosmoceros*, their own overcaution notwithstanding (11)]. Two forms of test have been fruitful. First, empirical studies of individual cases are now sufficiently voluminous to indicate general conclusions (see below). Ironically for Schopf and Hoffman, their three favorite cases of gradualism (forams studied by Malmgren and Kennett, mammals of the Bighorn Basin, and hominids) have all been challenged and interpreted as punctuational by additional or different empirical data (12). Their professed disproof of punctuated equilibrium in hominids (13) is, in fact, an example of a priori bias for gradualism. Cronin *et al.* (13, p. 116) document a trend in brain size as four clusters of points clearly permitting no distinction between alternative hypotheses of a single connecting line (phyletic gradualism) or several stepped events of speciation (punctuated equilibrium). Yet they write: "Any impulse to draw a step diagram through the points should be resisted."

Second, as pioneered by Stanley (10), estimates of aggregated change may be calculated and compared with data on

species number and duration for entire faunas to see whether transformation within lineages can account for observed change without invoking primary increments at rapid speciation events. Stanley concludes that phyletic evolution within lineages is too sluggish to account for much accumulated evolutionary change.

Punctuated equilibrium was proposed just a decade ago, but empirical case studies already point to general conclusions: high frequency of gradualism in single-celled planktonic organisms compared with high frequency of punctuated equilibrium in shallow-water marine invertebrates (2); higher frequency of gradualism in pelagic environments than in benthic environments (14). Punctuated equilibrium, particularly through its recognition of stasis as data, has greatly expanded the arena of evolutionary studies directly accessible to paleontologists. Eldredge and I are pleased that this theory about how speciation translates to patterns of geological time has generated so much fruitful empirical work.

STEPHEN JAY GOULD

*Museum of Comparative Zoology,  
Harvard University,  
Cambridge, Massachusetts 02138*

### References and Notes

1. T. J. M. Schopf, *Paleobiology* 7, 156 (1981); *Evolution* 36, 1144 (1982).
2. N. Eldredge and S. J. Gould, in *Models in Paleobiology*, T. J. M. Schopf, Ed. (Freeman, Cooper, San Francisco, 1972), p. 82; S. J. Gould and N. Eldredge, *Paleobiology* 3, 115 (1977).
3. G. F. Cuvier, *Recherches sur les Ossements Fossiles* (Peterville, Paris, 1812), vol. 1.
4. C. Darwin, *On the Origin of Species* (Murray, London, 1859).
5. H. J. MacGillivray, *Bijdr. Dierkd.* 38, 70 (1968).
6. R. A. Robison, *Fossils Strata* 4, 219 (1975); J. G. Johnson, *J. Paleontol.* 49, 646 (1975); D. V. Ager, *Proc. Geol. Assoc.* 87, 131 (1976); R. A. Fortey, *Skr. Nor. Polarinst.* (No. 160) (1974); J. L. Henry and E. N. K. Clarkson, *Fossils Strata* 4, 84 (1975); R. A. Reymont, *Paleobiology* 8, 293 (1982); A. Hallam, *ibid.* 4, 16 (1978); J. G. Johnson and W. W. Niebuhr, *Geol. Soc. Am. Bull.* 87, 1693 (1976); J. Roberts, *Lethaia* 14, 123 (1981).
7. P. G. Williamson, *Nature (London)* 293, 437 (1981).
8. P. C. Sylvester-Bradley, Ed., *The Species Concept in Palaeontology* (Publ. No. 2, Systematics Association, London, 1956).
9. Average species durations of more than 5 million years were estimated, with attempts to correct for biases in the fossil record, by D. M. Raup [*Paleobiology* 4, 1 (1978)] and S. M. Stanley (10). Empirical tabulations must err primarily in artificial shortness because imperfections of the record can only decrease duration by missing true earliest and latest occurrences, especially since species probably tend to be rare at their origin and near their demise. Schopf acknowledges this point but says it is swamped by the species of short duration that we miss altogether. I do not deny these total misses but point out that we can only work with what we have—and the empirical records of what we have are underestimates.
10. S. M. Stanley, *Macroevolution: Pattern and Process* (Freeman, San Francisco, 1979).
11. D. M. Raup and R. E. Crick, *Paleobiology* 7, 200 (1981).
12. For mammals, S. M. Stanley, *Evolution* 36, 460 (1982); for forams, G. M. Scott, personal communication; for hominids, G. P. Rightmire, *Paleobiology* 7, 241 (1981); L. Godfrey and K. H. Jacobs, *J. Hum. Evol.* 10, 255 (1981); R. E. Zindler, *ibid.* 7, 295 (1978).
13. J. E. Cronin, N. T. Boaz, C. B. Stringer, Y. Rak, *Nature (London)* 292, 113 (1981).
14. J. G. Johnson, *J. Paleontol.* 56, 1329 (1982).