



Istituto Veneto  
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## **Stephen J. Gould's Legacy: Nature, History, Society**

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*Stephen Jay Gould in the 1960s and 1970s,  
and the Origin of "Punctuated Equilibria"*

### **Abstract**

Steve Gould arrived as a beginning graduate student in the Department of Geology at Columbia University in the Fall of 1963. He was one of a group of entering students interested in paleontology, biostratigraphy, paleoecology and, of course, evolution. Though I was still an undergraduate, I was welcomed into the group – and took part in the field trips and special seminars they organized: especially one on paleontology and evolution whose main inspiration was Steve himself. Most of these students eventually went on to have distinguished careers in paleontology and related fields.

Steve's initial – and perhaps always his favorite – professional passion was morphology, development and evolution. He astonished everyone that he would devote an entire year away from his doctoral research to write an exploratory review paper on allometry – inspired by his initial work as an undergraduate with John White on the meaning of "b" in the famous equation  $y = bx^k$ . Steve quickly emerged as a model of the ambitious young professional, encouraging us all to develop and publish research projects – and to be bold and think about theoretical issues. He once said to me: Why wait until we are 60 before we publish on evolutionary theory? And of course he was right; indeed, sadly, he did not live beyond that very age.

The genesis of our 1972 paper *Punctuated Equilibria: An Alternative to Phyletic Gradualism* has been recounted several times, by Steve and by myself as well as by others. The definitive version, in my view, is in the newly published book *Rereading the Fossil Record* (2012) by historian David Sepkoski. I will review the essential details of our joint participation in Tom Schopf's GSA Symposium and multi-authored book, both entitled *Models in Paleobiology*.

Though the gist of the concept of punctuated equilibria was developed in my 1971 paper *The Allopatric Model and Phylogeny in Paleozoic Invertebrates*, both Steve and I added material developing and extending the concept beyond its bare essentials.

What were those essentials? Simply, the juxtaposition of the concept of allopatric speciation and the empirical demonstration of stasis – the fact that most species show little if any lasting morphological change throughout their often quite long histories. Change for the most part comes at speciation, and quiescence is the norm from then on in.

I will also add a codicil that I believe would have intrigued Steve very much: Darwin, as a young man in his late 20s, saw that the birth of species in isolation (the "allopatric speciation" of Dobzhansky and Mayr, so essential to our own notion of "punctuated equilibria") would account for the persistence of species, unchanged, "through thick formations" – in other words, our concept of "stasis". Darwin contrasted this vision with the inevitable gradual change of species – a vision of evolution he came to favor and promote, though he lacked empirical evidence for it.

With the birth of species in isolation, Darwin reckoned that adaptive change through natural selection happens rapidly in small populations. But with the passage of geological time and the inevitable environmental change that occurs, Darwin thought that natural selection would be constantly modifying entire species slowly and gradually. He could not reconcile the two views – and so his problem was deciding which was the most likely context for adaptation via natural selection to occur. He chose what we later called “phyletic gradualism”.

Darwin would have liked our title, but would probably have insisted on one minor change: *Punctuated Equilibria: The Alternative to Phyletic Gradualism*.

I think Steve would have enjoyed knowing that.