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Preface

May 20th 2012 was the tenth anniversary of Stephen Jay Gould's death. Palaeontologist at the Museum of Comparative Zoology, Harvard University, eminent evolutionary biologist, science writer, science historian and opinion maker, Gould gave us an extended and revised version of the theory of evolution, his "Darwinian pluralism", which is still today an interesting frame to understand the scientific advancements in many evolutionary fields. His anticipating insights about the conjunction of evolution and development, the role of ecological and biogeographical factors in "punctuated" speciation, the need for a multi-level interpretation of the units of selection, the interplay between functional pressures and internal constraints in processes like exaptations and spandrels are fruitful current lines of experimental research today.

Even his pungent and sometimes very radical controversies against the progressive representations of evolution (especially human evolution), biological determinism, pan-selectionist and a gene-centered view of natural history, or the adaptationist "just-so-stories", have left their mark in contemporary biology. Gould's "histories of nature" were explorations in the "nature of history," with wider cultural and philosophical implications, like his crucial concept of contingency. Thus, after 10 years of new discoveries and unforeseen advances, it is worthy to discuss the efficacy and limits of Gould's pluralism as renovation of the Darwinian research program.

At the historical location of the Istituto Veneto di Scienze, Lettere ed Arti in Venice, the town of Gould's "spandrels of San Marco", an international panel of scientists and philosophers—including Gould's closest friends and colleagues like Niles Eldredge, Elisabeth Lloyd, and (in video) Richard Lewontin—discussed his evolutionary and anthropological legacy, his idea of science as a complex rational enterprise, evolving itself and immersed in human society, his proposal for a methodology in historical sciences, and his unmistakable style of writing and argumentation, overcoming the boundaries between science, literature, and art. In Gould's production, scientific research and communication of science were two fields of inquiry strictly related by the idea that science is a high expression of human curiosity and culture.

The International Meeting was held at the Istituto Veneto, with the collaboration of University Ca' Foscari, on May 10–12th 2012. We thank Maria Turchetto

and Elena Gagliasso for their helpful participation in the organizing committee. The Venetian meeting has been the basis for the construction of this volume, which is divided into four parts. The first one—with the contributions of Niles Eldredge, Elisabeth Lloyd, and Telmo Pievani—is focused on the general scientific legacy of Stephen J. Gould as an evolutionary biologist: the unpublished history of the birth of Punctuated Equilibria; the role of Gould's criticism against adaptationism; the structure of his "Darwinian pluralism". The second part—with the contributions of T. Ryan Gregory, Alessandro Minelli, Gerd Müller, and Marcello Buiatti—is dedicated to the discussion of Gould's theoretical innovations seen from the perspective of genomics and developmental biology: the Gouldian idea of genome as a hierarchical system; the debate about the levels of selection and the "individual" units in evolution; his anticipations of some fundamental "Evo-Devo" concepts like developmental constraints and spandrels; his intuitions about the complexity of genetic coding and differential mutation rates. The third part—with the contributions of Ian Tattersall, Guido Barbujani, Klaus R. Scherer, and Winfried Menninghaus—deals with the important anthropological legacy of Stephen J. Gould: his advocacy of a highly branching phylogeny of hominids, against any progressive idea of cumulative change in human evolution; his bold fight against biological determinism and the alleged genetic foundations of the concept of "human races," the evolution of emotions, speech, and music in a Gouldian perspective. The fourth part—with the contributions of Andrea Cavazzini and Alberto Gualandi—is focused on some aspects of Gould's legacy in human sciences, with reference to the conceptual shifts between economics and evolutionary theory, and the possibilities and limits of Gould's humanism.

The richness of Gould's production and intellectual inheritance cannot be covered by a single collections of essays. Nevertheless, we hope to add another piece to the rich mosaic of studies that the Harvard evolutionist deserves. Gould's "industry" is a mine of historical hints, epistemological proposals, scientific insights, and contentious theories. As Richard Lewontin said in his thoughtful opening address by video conference, Gould's way of exploring evolution was a mix of pure history and theoretical generalizations, aided by extraordinary communicational skills and a worldwide reputation. He was so brilliant inventing metaphors (such as "spandrels" and "Punctuated Equilibria"), that he was able to depict for professionals, and for the general audience at the same time, the wide frame of the "multiple generating forces of evolution."

He was a forerunner. He challenged several orthodoxies, included the "ultra-Darwinian" one. He became a straw-man for many opponents. Still now, he is one of the most quoted evolutionists. During these first ten years his proposals and provocations have had a differential survival, but there are no doubts that his pluralism has strongly influenced the current debate. Stephen J. Gould is a present-day evolutionist.

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Part I
Evolutionary Theory

Stephen J. Gould in the 1960s and 1970s, and the Origin of "Punctuated Equilibria"

Niles Eldredge

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*

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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.

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."

That young 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.

1 Introduction

When Stephen Jay Gould died on May 20, 2002, he was arguably the most famous scientist in America, and perhaps in the entire world—ranking right up there with predecessors like Margaret Mead and Carl Sagan. Much of this fame was, of course, engendered by his so-called "popular" writing—but Steve told me long ago that successful writing styles do not change to embrace wider audiences: only the vocabulary changes. Steve felt that all of his writings, from the more narrowly technical to the most broadly engaging, were of the same intrinsic merit, reflecting fundamentally his same intellectual values. Steve owed his success, in large measure, to his skill in making his readers feel they are directly involved in his intellectual adventures.

But it was as fledgling paleontologists and evolutionary theorists that Steve and I first met, forging a lasting bond that, in less than a decade, produced what was probably Steve's—and my own—arguably most important and certainly well-known piece of scientific work: the theory of "Punctuated Equilibria." My goal here is to explore aspects of the educational experiences we shared, along with fellow students, in the Geology (and, to a lesser degree) Zoology Departments at Columbia University in the mid-1960s; to reflect on Steve's talents and proclivities as a young, career-minded scientist in those years; and to characterize the circumstances and, especially, the underlying evolutionary issues and empirical data that led to the publication of "punctuated equilibria" in the early 1970s. I will conclude with a brief analysis of the deep, if forgotten, intellectual roots of Punctuated Equilibria—concluding that both allopatric speciation and what we called punctuated equilibria, both clearly conceived by Darwin but never published, simply had to be rediscovered and elaborated on in the 20th century.

2 Steve Gould's Impact on Fellow Fledgling Paleontologists at Columbia in the 1960s

Steve Gould showed up on the Columbia campus in the Fall of 1963, newly-graduated from Antioch College, and now-enrolled in the invertebrate paleontology program at Columbia's Department of Geology. He was joined, significantly, I think, by at least a half-dozen other aspiring paleontologists or stratigraphers—among whom was H. B. Rollins. Most of these new students went on to have productive and distinguished careers. I think the sheer size of this entry class was critical to the dynamics of the learning process—as they did, as students often do, take their intellectual life largely into their own hands.

In the Fall of 1963, I was a junior in college, and having decided that I would stay in the academic world, I was trying to make up my mind whether I would go into physical anthropology or geology/paleontology. I was smitten by this intellectually active new group of graduate students—and was delighted that they let me hang around. John Imbrie was then the invertebrate paleontologist on the Columbia campus (with Norman D. Newell and Roger L. Batten, at the American Museum of Natural History, acting as adjuncts within the Columbia Geology Department). I was taking Imbrie's introductory paleontology, followed the next semester by biostratigraphy, which was open to graduate students.

But the really important thing was that, probably with Steve as ringleader, the new graduate students saw that there was little in the way of evolution in the curriculum. So, they started their own seminar, and they let me join in. We read extensively, and, taking turns, each of us led discussions. At one point I did a session on macroevolution. This was when Steve's influence on all of us quickly emerged. He believed that no one should wait until they are sixty (ironically, his age when he died) before they start actively thinking, talking and writing about theoretical issues. And, for that matter, publishing on them!

Paleontology, then as now, was usually split between invertebrate and vertebrate programs—and at Columbia, at least, vertebrate paleontology, ever since the days of Henry Fairfield Osborn in the last decade of the nineteenth century, lay in the province of the Zoology (now Biology) Department. Vertebrate Paleontology was seen as the more intrinsically biological subject—with its focus on the anatomy of fossil bones, and their relevance to deciphering phylogenetic relationships. That was the supposed route to take if one wanted to contemplate evolutionary issues from the standpoint of the fossil record.

In contrast, invertebrate paleontology was usually pursued in geology departments; certainly this was always the case at Columbia. Though some invertebrate paleontologists—including Norman D. Newell, who was mentor to both Steve and myself—had active interests in ecology and evolution, traditionally invertebrate paleontology had been studied largely as a means of correlating rocks, thus producing a repeatedly tested framework of geological time. And though much of the interest in this aspect of invertebrate paleontological research lay in its economic implications for the search for oil and gas reservoirs, the discipline of biostratigraphy (the spatio-temporal distribution of species in the fossil record), especially as developed in the nineteenth century in Europe going all the way back as far as Cuvier, had clear implications for understanding patterns—thus potentially processes—of evolution.

Why did Steve Gould, so famous for having fallen in love with the American Museum's *Tyrannosaurus* at age 5, decide to pursue invertebrate paleontology rather than the more traditionally biologically and evolutionarily-minded vertebrate paleontology? I think the main reason was simply Steve's undergraduate experience with the invertebrate paleontologist J. F. White at Antioch. Steve's very first paper (published as White and Gould 1965) was on the meaning of "b" in the famous equation $Y = bX^k$, used variously to describe allometric growth of individuals, series of individuals within populations—or even evolutionary changes between closely related species in a lineage. Steve had discovered (or Prof. White had shown him) an unwrapped, unstudied collection of Bermudan Pleistocene land snails in the basement of the Geology Department at Antioch—and Steve had been smitten with the geometric growth of these well-preserved snails—and had vowed to one day make them the subject of his doctoral dissertation. Few people arrive at graduate school already knowing the precise topic of their future Ph. D. dissertation!

A glance at Steve's earliest entries on his prodigious bibliography reveal his passion for growth and form, and for morphology in general. We were all aghast when Steve took an entire year off from his doctoral research to answer the invitation from the journal *Biological Reviews* to write a review of the literature on allometry—an opportunity Steve used to make fresh observations on the subject, especially its relationship to evolution (Gould 1966). Steve saw that invitation as a golden opportunity—and, as was to be his hallmark, he jumped on the chance and worked extremely hard on it. I have always said that I never met anyone so smart who worked so hard as Steve Gould. He was establishing a reputation as an original thinker on theoretical issues—and laying the groundwork, both in substance and style, for his first book *Ontogeny and Phylogeny* (Gould 1977).

Thus Steve, at heart, was first and always a morphologist and developmentalist. One of his most important and original insights came towards the end of the

1970s—when he was among the first to point out that regulatory genes, depending upon their actions, and when in ontogeny they are switched on, can have a disproportionately large effect in modifying adult morphologies in the evolutionary process: long-since a central tenet of evolutionary developmental biology—or "evo-devo."

And, I must also say, in an evolutionary context, Steve was as much of an adaptationist as the next person. I know it sounds strange to say so, given his reputation as a critic of hyperadaptationism—and his search for alternative explanations for morphological change in evolution (as witness his enthusiasm for Elisabeth Vrba's concept of "exaptation"—published as Gould and Vrba 1982—though the initial idea had been developed by Vrba). All that is true—but at heart he was a neo-Darwinian always. As am I—and so are we all.

Once, after a seminar at the American Museum sometime after 1965 (when I had graduated from Columbia College and had taken my own place in the Columbia graduate program), he said in mock-serious despair "sometimes I think that man will renounce natural selection on his death-bed"—referring to our august mentor Norman D. Newell, who seemed to include everything but natural selection when discussing the history of life, and how it all came to be, with his students (Fig. 1).

Newell, we were slowly beginning to realize, was the only person in the mid-twentieth century who took patterns of what we now call "mass extinctions" seriously—and insisted that they deserve special study to elucidate their causes

Fig. 1 Stephen Jay Gould (*left*) and Niles Eldredge (*right*) flanking their mentor, Norman D. Newell (*seated*) on the occasion of Dr. Newell's 90th birthday celebration at the American Museum of Natural History in New York in February, 1999. Photo by Gillian Newell

(e.g. Newell 1963). He also insisted that they periodically have an enormous impact (literally and figuratively) on the history of life, thus opening the door still further to seeing a causal interrelationship between evolution and its converse: extinction.

For a time, we callow graduate students openly wished Newell would discuss evolution—not extinction. Emphasize the positive, not the negative! And it was only later—indeed, not until the 1980s—when we were immersed in our professional pursuits at different institutions, that the Alvarez hypothesis on the end-Cretaceous mass extinction made such headlines, and it began to become clear that much, if not all, evolution occurs only after episodes of ecosystem disruption, sufficiently widespread and severe to cause the extinction of entire species—and in the most dramatic and easily seen cases—of higher taxa.

But how, exactly, to study evolution in the invertebrate fossil record? After all, with just the remains of their exoskeletons, it was often hard to discern the adaptive significance of much of the morphology of invertebrate fossils.

No one back in the 1960s knew that evolutionary theory literally had begun with the work of Jean-Baptiste Lamarck in France (Lamarck 1801; also 1809) and Giambattista Brocchi in Italy (Brocchi 1814; see also Dominici 2010 and Dominici and Eldredge 2010)—both of whom had brought a quantitative aspect to their consideration of Tertiary fossil mollusks. But, on the other hand, Norman Newell had already conducted several studies on evolutionary lineages in Upper Paleozoic bivalves in the 1930s and 1940s (e.g. Newell 1938, 1942)—and Tom Waller, an older graduate student working under Newell at the American Museum, was already deeply immersed in a detailed study of scallop evolution in the Tertiary Atlantic and Gulf coastal deposits of North America. Tom was using bivariate statistics as a cornerstone of his characterization and comparison of scallop morphologies in space and time.

And then there was the simple fact that it was the 1960s—and computers were just appearing on major university campuses. Columbia got its first IBM 7090/7094 computer system sometime around the mid-1960s, and many of us soon found ourselves scurrying over to the Computer Center clutching shoeboxes crammed with those old IBM punch cards. And we were lucky that John Imbrie, picking up on the newly found passion for multivariate statistical analysis then beginning to infiltrate geology in general, introduced all of us who were adventurous to the intricacies and potential analytic power of Factor Analysis, Multivariate Analysis of Variance, the Mahalanobis D^2 statistic—and other arcane statistical delights. Steve was already immersed in statistical analysis with his interests in allometry—and my second published paper (Eldredge 1968) was entitled *Convergence of Two Pennsylvanian Gastropod Species: A Multivariate Mathematical Approach*.

In short, circumstances themselves converged to cry out for studies of evolution in the fossil record. We quickly saw that, whatever the disadvantages that many invertebrate fossil taxa have for old-fashioned evolutionary studies purporting to document adaptive change through time, these were more than outweighed by the availability of statistically meaningful samples in well-chosen study groups.

And one more factor played a key role in these studies: Dobzhansky and Mayr, still dominant figures, had shown in the 1930s and 1940s (e.g. Dobzhansky 1935, 1937; Mayr 1940, 1942) the critical importance of geography and isolation in the evolutionary process. It would be as important to study patterns of geographic variation in more or less contemporaneous populations within a lineage—as it would be to chart the course of morphological change (and, as it quickly turned out, the non-change we later called "stasis") through time.

Steve stuck to his guns and did his Pleistocene Bermudan land-snails—calling it (in an early example of the apt, often perfect, metaphors he became famous for) a "microcosm." The snails were isolated there on this small island, preserved in sediments reflecting two contrasting sorts of environmental conditions. He had no idea that, in studying fossils of a lineage of which there were still-living, surviving species, he was actually working on what I have come to see as the Ur-question of evolutionary biology: the search for a natural causal explanation for the origin of the species comprising the modern biota.

In contrast, I went to the Paleozoic—a disadvantage, as the old-timers like Brocchi saw, because none of the species present as fossils in the Devonian had anything directly to do with the origin of our modern fauna. But I had complex anatomy (my fossils were trilobites), and large populations spanning nearly half the North American continent in breadth, as well as prodigious amounts of geological time (6–8 million years—now considered to have been closer to 6 than 8 million years).

In a nutshell, I found that my trilobites—my *Phacops rana*—showed such stability, such lack of change through time, that I despaired of finding any evolution at all. But I saw it happening laterally, and it was clear that the allopatric model—geographic speciation—was the only way to make sense of my patterns in terms of modern evolutionary theory. I wrote these conclusions up in my Ph. D. thesis (Eldredge 1969), and I took that material and revamped it for the journal *Evolution*, submitted in 1970 and published as *The Allopatric Model and Phylogeny in Paleozoic Invertebrates* (Eldredge 1971) (Fig. 2).

Meanwhile, Steve had finished his evolutionary analysis of different stocks of *Poecilozonites* (later published as Gould 1969)—and, in 1968, headed off to begin his impressive career at Harvard—where he joined that rarified group of evolutionary biologists that included Ernst Mayr, Dick Lewontin and E. O. Wilson, and overlapping just briefly with the great evolutionarily-minded paleontologist George Gaylord Simpson.

I, in contrast, happily stayed in New York, accepting an appointment as an Assistant Curator in the Fossil Invertebrates Department at the AMNH, and an Adjunct Assistant Professorship at Columbia, in 1969.

Thus our days of occupying nearby offices in Schermerhorn Hall at Columbia, attending seminars at the AMNH—and, perhaps most critically—riding back and forth between Columbia and the Museum several times a week on the #11 bus, were over. Those bus rides were amazing. Almost invariably, Steve would launch into a soliloquy, telling me a story about something or other he had recently read—something intriguing to him that he had picked up in the literature. These rides

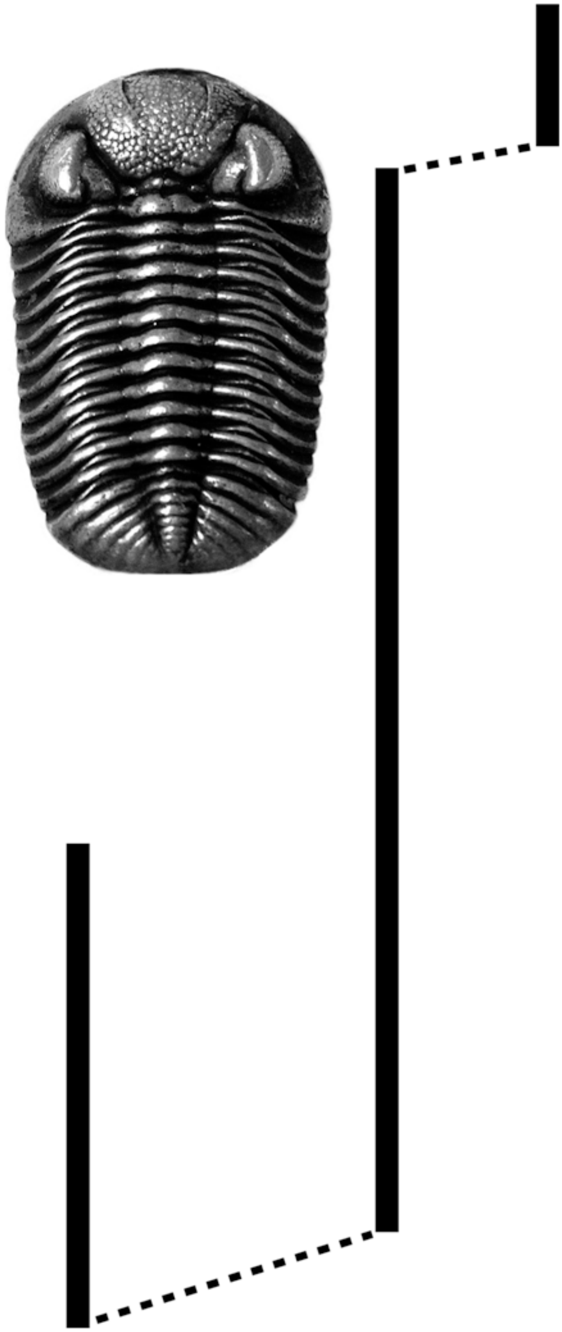

Fig. 2 The evolution of the Devonian trilobite *Phacops rana* lineage—the original empirical example of "punctuated equilibria"

were invariably entertaining and sometimes astonishing. So I had no trouble at all, when the editor of *Natural History* magazine asked me if I could recommend someone to replace his outgoing columnist (my earlier mentor and role model, the anthropologist Marvin Harris); without giving it a second thought, I said "Steve Gould. He's never at a loss for words and always has a good story to tell"—or words to that effect.

But if the old student days together, with our wives and fellow students, were over, my working relationship with Steve in a very real sense was just getting going.

3 Punctuated Equilibria

Both Steve and I (e.g. Eldredge 2008), as well as others, have written on the history of the production of the actual paper we entitled *Punctuated Equilibria: An Alternative to Phyletic gradualism*—published as Eldredge and Gould 1972 in a multi-authored book entitled *Models in Paleobiology*, edited by invertebrate paleontologist Thomas J. M. Schopf. Fortunately, what I consider to be the definitive, canonical history of the circumstances and events—including a detailed analysis of the manuscript as it went through its pre-publication revisions, specifying in detail who wrote what when—has just been published by historian David Sepkoski (Sepkoski 2012) in his important new book *Rereading the Fossil Record. The Growth of Paleobiology as an Evolutionary Discipline.* Sepkoski reports that, as the son of the late Jack Sepkoski—a marvelous early developer of quantitative, "taxic" paleobiology, and one of Steve Gould's first graduate students—he was perhaps especially privy to the files and archives pertaining to the development of the entire discipline in the 1970s and 1980s, including the early contribution of "punctuated equilibria." I find his account lucid and accurate—and written with the dispassionate eye of an excellent historian. Indeed, it is somewhat prepossessing to find one's own actions, and those of his colleagues, from so long ago, described so truthfully—and, to me—as if it had happened just yesterday. Steve, I am sure, would have felt the same way had he survived to read David Sepkoski's book.

So the details are all out there and readily available, and I need not belabor them here—except to sketch briefly a few of the most basic points. For more information, readers should consult Sepkoski's book; as I am sure Steve would agree, in the immortal words of New York Yankes manager Casey Stengel, now "you could look it up"!

Steve, as I have said, had departed for Harvard—and was well on his way, working, if anything, harder than ever and participating as fully as possible in intellectual activities within—and even beyond—the strict confines of paleontology. Steve got wind of Tom Schopf's plans to organize a symposium for the 1971 Geological Society of America annual meeting, coupled with a book of the same title to be published afterwards. Hoping to join in, Steve unsurprisingly asked for the title "Models in Morphology," or perhaps "Models in Phylogeny." Schopf told him that Dave Raup had already accepted the morphology assignment, and

Michael Ghiselin the one on phylogeny. Steve had to take the next best thing, so far unassigned: "Models in Speciation."

Steve evidently thought about it—and then, getting in touch with me, said something to the effect that he couldn't think of much else to say beyond what I had written already and sent to him for comments—namely, the "Allopatric Model" manuscript that was published in 1971 in *Evolution*. He asked me to be coauthor and I said "sure"—and either then, or shortly thereafter, he proposed that he give the talk at the meeting and be senior author of the GSA meeting abstract, while I would write the initial draft of the full paper, and be senior author, of the published version of the paper. Sounded OK to me: I didn't especially like giving talks, as Steve unnecessarily reminded me—and in any case it always seemed far better to be senior author of a published paper than of an abstract of a talk at a symposium.

I was already thinking that the two papers held the potential of igniting a lot of interest and perhaps controversy—in paleontology, but also in evolutionary theory: primarily because one of the claims, based on empirical evidence and held out to be general, deviated far from the norm of conventional thinking. About which more below.

I wrote that first draft—including an account of Steve's thesis research on Bermudan snails, cast explicitly now into the context of the two main thematic components of our proposed theory. I also added an extra discussion, not previously agreed upon with Steve, on what I saw was a major implication of punctuated equilibria.

Steve came back with a greatly expanded essay, improving the rhetoric, making the argument more forceful, clarifying some concepts, and adding some thoughts on macroevolution of his own. And, crucially, he named not only the theory itself ("Punctuated Equilibria"), but also the phenomenon of species stability through long periods of geological time ("stasis"), as well as the vision of adaptive evolutionary history comprising inexorable gradual modification of entire species through time ("Phyletic Gradualism"). There is a lot to names, and our title, *Punctuated Equilibria: An Alternative to Phyletic Gradualism*, given what I just said about Steve's bestowal of names, was entirely Steve's.

I must say, however, that late in his life I asked Steve about why he had started calling our baby "punctuated equilibrium" instead of the original "punctuated equilibria." At first he affected not to understand what I was talking about, and basically denied having done so. Whatever the reason, I personally detest the term "punctuated equilibrium."

So what were the two thematic components of "punctuated equilibria?" (Fig. 3). Firstly, and contrary to popular and professional belief, and contrary especially to the enduring message of Charles Robert Darwin, we postulated that there is little if any empirical evidence that entire species will change slowly, gradually and progressively through geological time—such that new species in general evolve gradually from old. Phyletic gradualism is *not* a valid general model for the generation of morphological change, adaptive or not, in the evolutionary history of life. Rather, species, however variable locally and

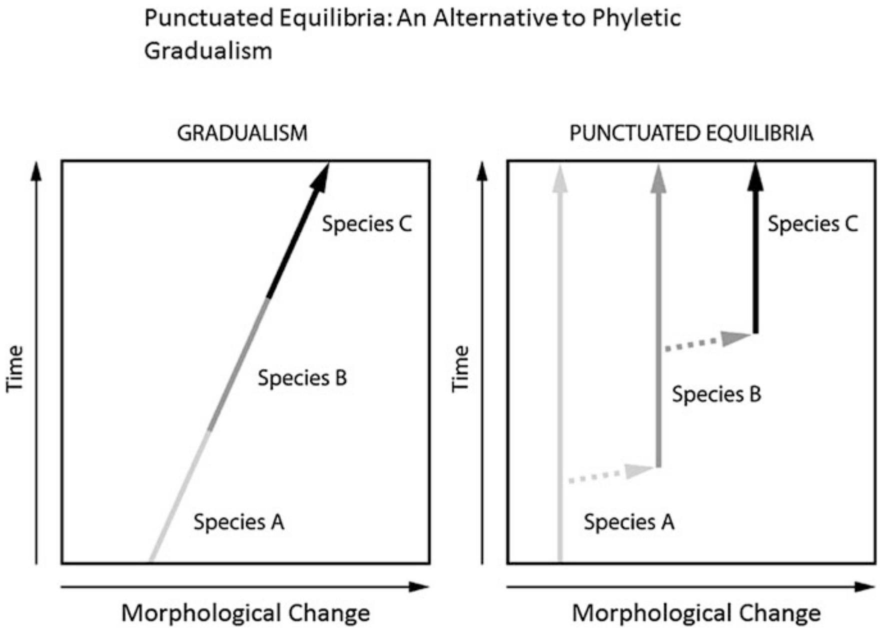

Fig. 3 Comparison of "phyletic gradualism" and "punctuated equilibria" evolutionary patterns

geographically, typically do little more than oscillate (in terms of mean values of this or that morphological attribute) through what can be astonishingly long periods of time—in the case of marine invertebrates usually 5 million years or even longer. This is what we meant by the term "stasis."

As to the second component, it was simply the application of Dobzhansky and Mayr's notion of geographic ("allopatric") speciation: the origin of new species, with at least a modicum of adaptive change, usually if not invariably detectable on the morphological level, to explain the appearance of species from "offstage"—from elsewhere; and the common, continuing pattern of geographic replacement of closely related species or even what Darwin used to call "varieties." Morphological change in conjunction with the origin of new species in isolated populations—a documented phenomenon in the modern fauna, thanks to the work of Dobzhansky, Mayr and all who followed—simply must have been working as the norm throughout the history of complex life.

The section I had added to my original manuscript on the importance of considering geographic speciation when addressing evolution in the fossil record, addressed an apparent paradox: if our thesis is "true," and if phyletic gradualism in the main paints a false picture of the evolutionary process, how do we explain evolutionary trends in the fossil record—such as the net increase in brain size in hominid evolution over the past few millions of years? After all, long-term, essentially linear "orthoselection" was ruled out in our model.

That section concluded that there is a de facto pattern of net survival of some species over others (Fig. 4), based on the phenotypic properties of individuals within those species, that could well yield the trends we seem to see in the fossil record. And that, of course, was the harbinger of many debates of species selection, Vrba's (1980) "effect hypothesis," and hierarchical thinking in general.

And, sure enough, there was a big reaction to our paper—among our colleagues in the paleontological realm and, increasingly, in larger biological circles. Of course we were happy for the relatively few who congratulated us on finally bringing paleontology out of the dark ages; others said they knew it all along (which may or may not have been true)—while still others castigated us for being the ignorant renegades they took us to be.

It was Steve's final rewriting and his consistently bold rhetoric which really did the trick—in terms, at least, of commanding attention, if not universal approbation. We had posted a manifesto that could not be ignored—unlike my 1971 *Evolution* paper that had basically sunk without a trace.

At Steve's urging, we (Gould and Eldredge 1977) wrote a "where are we now?" follow-up paper five years later, publishing it in the newly-fledged journal *Paleobiology*. Steve wrote the entire manuscript, inviting me to add, delete and so forth. But all I ended up doing was sitting with him one afternoon in his motel room at yet another autumnal GSA meeting, arguing about one single—but, to my

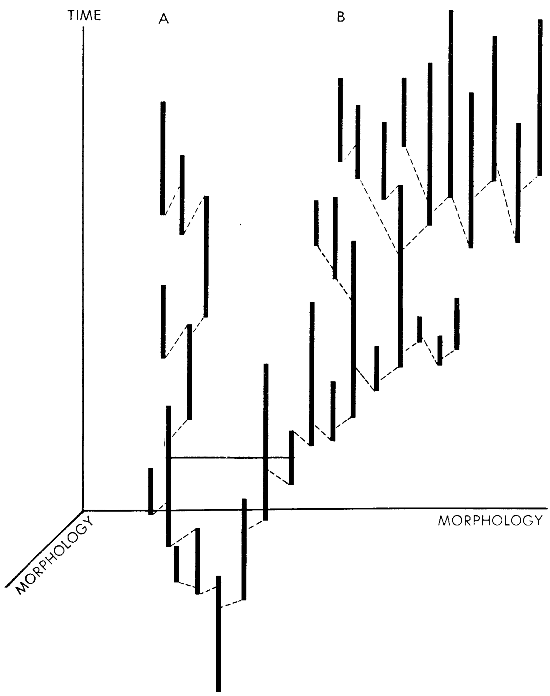

Fig. 4 Differential production and survival of species within two related clades. Reproduced from Eldredge and Gould (1972)