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Stephen Jay Gould, Jack Sepkoski, and the 'Quantitative Revolution' in American Paleobiology

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Abstract. During the 1970s, a "revolution" in American paleobiology took place. It came about in part because a group of mostly young, ambitious paleontologists adapted many of the quantitative methodologies and techniques developed in fields including biology and ecology over the previous several decades to their own discipline. Stephen Jay Gould, who was then just beginning his career, joined others in articulating a singular vision for transforming paleontology from an isolated and often ignored science to a "nomothetic discipline" that could sit at evolution's "high table." Over the course of a single decade, between 1970 and 1980, this transformation had in large part been accomplished. Among those most centrally involved in this process were Gould, Thomas Schopf, David Raup, and Gould's graduate student Jack Sepkoski, all of whom made major contributions in theoretical and quantitative analysis of the fossil record and evolutionary history. Recognizing that an ideological agenda was not enough, Gould and others developed and promoted new outlets, technologies, and pedagogical strategies to nurture their new discipline. This paper describes this process of transformation, and presents Sepkoski's education and participation as exemplary of the "new model paleontologist", which Gould hoped to produce.

Keywords: J. John Sepkoski, Jr., paleobiology, paleontology, statistics, Stephen Jay Gould

Introduction

As a number of scholars have noted, the development of paleontology in the United States during the 20th century was marked by a tension with its more glamorous cousin, biology. This was particularly the case in the arena of evolutionary theory: despite the efforts of paleontologists like George Gaylord Simpson in the 1940s and 1950s to promote greater understanding and collaboration with geneticists, such understanding was slow in coming, and paleontologists were often looked upon by biologists as mere cataloguers rather than equals. Simpson's work in such classics as *Tempo and Mode in Evolution* and *Major Features of Evolution* did certainly attract attention from biologists, and it played an important role as inspiration to a later generation of paleontologists who were prepared to challenge the status quo in evolutionary science.[1] Nonetheless, Simpson's own approach to the possible synthesis between the two disciplines was somewhat conservative, and he was ultimately content to let paleontology play its part as handmaiden to genetics.[2] This is hardly surprising, given the fact that the modern evolutionary synthesis, articulated by Ernst Mayr, Theodosious Dobzhansky, Simpson, and others, treated genetic mutation and gene frequency as the major components of natural selection.[3] As Simpson himself acknowledged, paleontology simply does not have access to these data. The prominent English geneticist John Maynard Smith put the attitude of his colleagues succinctly: "the attitude of population geneticists to any paleontologist rash enough to offer a contribution to evolutionary theory has been to tell him to go away and find another fossil, and not to bother the grownups."[4]

The operative phrase in the last quotation, however, is "has been." The passage is taken from an opinion piece that Maynard Smith wrote in *Nature* in 1984 in which he was actually *praising* the recent contributions of paleontologists to evolutionary theory. He concluded the essay with the magnanimous proclamation, "the paleontologists have too long been missing from the high table [of evolution]. welcome back."[5] Why was Maynard Smith, one of the most aggressive proponents of the genetic basis for the modern synthesis, prepared to open the doors to paleontology after a fifty-year hiatus? He himself cited the work "of a group of paleontologists" led by Stephen Jay Gould who had introduced important theoretical modifications to the theory of natural selection during the previous 10 years. Most notably, he pointed to the concept of "species selection" (a particular favorite of Gould's) as a novel contribution to evolutionary theory, which, he argued, was analogous to the selection mechanisms for genes and individuals within a population.

[1] See Rainger, 1988; Cain, 1992, 1993, and 2002; Smocovitis, 1992; Ruse, 1999a; Simpson, 1978; Laporte, 2000.

[2] For example, in the introduction to the first edition of *Tempo and Mode*, Simpson wrote that paleontology's main contribution to evolutionary theory was to correlate paleontological evidence about the tempo and mode of evolution with the mechanisms of the geneticists. Simpson, 1944, pp. xv–xviii.

[3] The literature concerning the modern synthesis is vast. Prominent examples include Mayr, 1942 and 1982; Dobzhansky, 1953; Provine, 1971; Gould, 2002; Smocovitis, 1996.

[4] Maynard Smith, 1984, p. 401. Smith also noted that Simpson's "role was to show that the facts of paleontology were consistent with the mechanisms of natural selection and geographical speciation proposed by the neontologists… rather than to propose novel mechanisms of his own."

[5] Smith 1984, p. 402.

Maynard Smith's comments reflected a growing consensus in the biological community that paleontology could, in fact, make important contributions to evolutionary theory – particularly in the area of macroevolution. Four years earlier, in 1980, an important symposium was held at the Field Museum of Natural History in Chicago in which population biologists, molecular geneticists, and paleontologists met to discuss this subject. The conference was hailed as a turning point by many of its participants, and was given prominent mention by the science writer Roger Lewin in *Science*.[6] Maynard Smith was present, as was Gould, along with a host of established scientists from the various disciplines represented. Maynard Smith was not alone among the geneticists in welcoming the work of paleontologists such as Gould: in reference to Gould's macroevolutionary analysis of the fossil record, Francisco Ayala remarked "we could not have predicted stasis from population genetics, but I am now convinced from what the paleontologists say that small changes do not accumulate."[7]

This détente between genetics and paleontology has been hailed as "revolutionary" and "historic" for the study of evolution. What Maynard Smith and others were perhaps slow to acknowledge, however, was that it was not founded just on a decade's worth of activity by a few scientists, but rather had been building since at least the late 1950s in the work of a small but influential group of paleontologists. This group was largely produced by the graduate programs at Yale, Columbia, and Harvard who were committed actively to adapting techniques, methods, and models from biological disciplines, including – most significantly – applying quantitative and statistical techniques to the study of macroevolution. Gould was indeed the most prominent figure in the younger generation of this movement, but he relied heavily on collaboration with colleagues like David Raup (1933) and Thomas Schopf (1939–1984) in the late 1960s and early 1970s, who contributed vision and expertise that complemented Gould's own agenda.[8] As a young professor at Harvard, Gould also recruited talented graduate students who were exposed to a wide range of interdisciplinary training to help carry out the mission of transforming paleobiology into "a more nomothetic, evolutionary discipline" via adoption of biological models and the development of new quantitative techniques.[9]

[6] Lewin, 1980, pp. 883–887.
[7] Lewin, 1980, p. 884.
[8] For a detailed narrative of the scientific and pedagogical history of paleobiology between the 1950s and the 1970s, see Princehouse, 2003, especially chapters 4 and 5.
[9] "Nomothetic" simply means "law-producing."

One of Gould's first students was Jack Sepkoski (1948–1999), who, both in his work with Gould at Harvard and later as a colleague of Raup and Schopf's at the University of Chicago, played an instrumental role in making this vision a reality. In the spring of 1971, Gould wrote to Sepkoski, who had just joined the program at Harvard but was considering to leave his study with Léo F. Laporte at UC Santa Cruz. Sepkoski had expressed concern with finding an appropriate thesis director at Harvard, and felt his interests in "paleoecology, paleoenvironments, and carbonate sedimentation" would be best served by Laporte. He had also mentioned a desire to leave the "pressure-cooker" environment of Cambridge for the "relaxed, personable atmosphere" of Santa Cruz.[10] Gould's response – which was ultimately persuasive – is particularly revealing, and is worth quoting at length:

> There is not a better man than Leo in that particular little area of Paleozoic paleoenvironments. Neither can I deny that there is probably more joy in California, both in the sun (literally and metaphorically) and in Leo's vitality and group approach vs., for example, my own kind of pedantry and reverence for an antiquated type of individualized scholarship. But Harvard does have considerable advantages. With a combination of people (including Siever, for example), you can surely gain advisers equal in ability to what Leo does by himself... But the main reason for Harvard is not this; it's rather the potential, if you seek it, for the most important ingredient in scientific innovation: stimulation from intelligent men in related fields. If you're just surrounded by geologists with geological training, you will do little more than an elegant piece of work along lines already explored. But there's a revolution going on in ecology and biogeography. It's related to an approach via deductive models (that you can comprehend, and many others of our grad students cannot) and much of it is centered at Harvard (Wilson, Bossert; and it will be firmly lodged here if, as rumor (in the usual sense) has it, McArthur comes here). The next great innovator in paleoecology will be the man who successfully learns to understand this revolution and transfer its insights into paleontology; it will not be the man who pursues geological study with geologists, however excellent.[11]

[10] Draft of letter, J. John Sepkoski, Jr. to Robert Garrison, April 18, 1971. Unless otherwise noted, references to unpublished papers are from the J. John Sepkoski, Jr. papers at the American Philosophical Society, Ms. Coll. 111.

[11] Stephen Jay Gould to Sepkoski, April 28, 1971. Sepkoski Papers, Box 10–3.

As a statement concerning the current and future directions of the fields of paleontology and paleobiology, this letter makes several claims and predictions that can be examined historically. Together, these claims amount to a clear vision, *in utero*, of Gould's programmatic agenda for transforming the discourse and status of paleontology. As a case study, Sepkoski's response to this challenge illustrates the ways in which young, quantitatively-minded and computer-literate paleontologists were encouraged to participate in this vision.

Broadly speaking, the "revolution" that Gould mentioned involved four aspects that would help transform paleontology over the next 10 years, and Sepkoski was positioned to take advantage of these for some very distinct reasons. The first involved the use of quantitative and statistical methods to model patterns in evolution and diversity using data from the fossil record. These were the "deductive models," that Gould mentioned in his letter, and they were made possible by advances in computer technology and techniques that allowed powerful multivariate analysis of large data sets. Sepkoski indeed possessed tools to perform this kind of work that many of his fellow students did not have, and his technical abilities in this area – knowledge of computer programming, facility with multivariate statistics – and willingness to share his expertise gave an important boost to his early career. These were skills that were not drawn from the standard paleontology graduate curriculum (although through the 1970s they became established in many programs), but rather were gained from an independent and eclectic study of other disciplines, including mathematics, computer science, ecology, and biogeography. Sepkoski benefited particularly from coursework as an undergraduate at the University of Notre Dame, where he majored in geology but had significant exposure to statistics, computer programming, and mathematics, under the guidance of Ray C. Gutschick.

The second factor involved the application of biological models to paleontology. Sepkoski set himself a rigorous program of self-study in ecology, multivariate statistics, and diversity analysis that surveyed a wide selection of current ideas in these fields covering the period from about 1964 to 1971. In the early 1970s, Harvard was indeed a place where these kinds of multidisciplinary interests and insights could be nurtured, and Sepkoski benefited in particular from study with E.O. Wilson and William Bossert. From these teachers, he learned the fundamentals of population biology and dynamics, which he would later help to apply directly to macroevolution. Wilson and Bossert's approach to the subject was highly quantitative, and Sepkoski's eventual insight was to superimpose their equations for the dynamics of individual, living populations onto the fossil record.

Third, Sepkoski benefited from fortunate timing. The early to mid-70s were propitious years to be a young paleontologist with a statistical, deductive bent and an interest in biological models. Paleontologists including Raup and Schopf were beginning to publish quantitative analyses of species diversity that drew heavily on population biology. Among this group of scientists, an intuition was developing that deductive models could reveal new patterns in evolution and extinction. There were also new outlets for these ideas, including the journal *Paleobiology*, which Schopf founded in 1975, that actively encouraged publication by young scientists with innovative and interdisciplinary insights. Collaboration was essential to this enterprise, because the computer routines developed independently by the few capable workers in this area needed to be tested and cross-checked against different data sets, and the data needed for reliable statistical computation were too massive to be collected by any one person. Sepkoski in particular benefited from this collaborative aspect: early on in graduate school he was being consulted on technical questions by some of the leading figures in this field, and his quantitative skills were instrumental in landing positions at the University of Rochester and the University of Chicago even before his dissertation was completed.

Fourth, Gould's own vision of the pattern of evolution – which was unveiled a year after the letter quoted above – relied on many of the insights that were being produced by the statistical and deductive models of the quantitative paleobiologists. As described in his papers with Niles Eldredge on ''punctuated equilibrium'' and expanded in later professional and popular works, this vision called for nothing less than a challenge to the received picture of the 'tempo and mode' of evolution that grew out of Darwin's writings and the evolutionary synthesis of the 20th century.[12] Specifically, Gould wanted to challenge the gradualist evolutionary model by emphasizing the syncopation and discontinuity in rates of speciation and extinction, that he believed he had detected in the fossil record. The trouble was that Gould's argument rested on an intuition only; there were too few reliable data for the entire fossil record, and what evidence there was could not be conclusively proven to

[12] While the modern synthesis was a through revision of classic Darwinian evolutionary theory, it shared one important feature with the original model: a gradual and uniform tempo of speciation. Both models assumed that the fossil record was incomplete, and that the gaps represented in the record were artifacts of its imperfection. The genetic basis of the modern synthesis provides the mechanism for inheritance that Darwin's model was missing, but is consistent with its uniformitarian framework. Speciation happens over a long period of time, as the frequency of particular mutations within a population gradually accumulate.

be representative. Another difficulty was that while Gould had done important work using quantitative methods, he was by his own admission less comfortable with advanced statistics and computer programming than some of his colleagues.[13] He could, however, encourage bright young students like Sepkoski to take up these methods, and could guide them towards questions that would help establish his larger theoretical vision – such as statistical analysis of fossil data that could determine whether or not the patterns shown in the existing record were artefactual. In the later 1970s and 1980s, he was also in a unique position, as eminent popularizer and spokesperson for paleontology, to forcefully support the results of quantitative research, and Gould missed no opportunity to integrate them into his own grand vision, both in his scientific work and, increasingly, in his columns in *Natural History*. This was particularly the case in the 1980s, when Gould widely promoted the theory of "periodicity" in extinction developed by Sepkoski and others that was in many ways a fulfillment of the promise Gould handed to Sepkoski in his letter in 1971.

This paper will examine the four aspects described above, in order to shed light on an important transitional moment in the history of recent paleontology. This moment crystallized a convergence of factors: the emergence of powerful new quantitative techniques for the development of deductive models, a conducive pedagogical environment at Harvard in the early 1970s, heightened interdisciplinarity among a younger generation of paleontologists and a willingness to look to other disciplines for methodological insights, and finally Gould's promotion of a grand theoretical framework with which to mount a frontal attack on contemporary evolutionary theory. The results of this moment were far-reaching, both for paleontology as a discipline, and for evolutionary theory in general. By the early 1980s, quantitative methods were increasingly part of the formal curricula in many paleontology programs in the US and abroad, and this was a direct result of work done in the 1970s by people like Sepkoski, who went on to teach courses on the subject and to advise students who practiced the methods. The generation trained in the 1970s has multiplied itself geometrically in the 1980s and 1990s, and the quantitative approach is now firmly established in the field. The insights of those first generations have also had a hand in transforming current understanding of the patterns and mechanisms of evolution. As Patricia M. Princehouse has convincingly argued, the

[13] Regarding his mathematical abilities, Gould claimed "I'm not very good in mathematics. I'm really not…. [but] I can see patterns in things, different kinds of scale secants." Nonetheless, his mathematical skills were sufficient to teach basic techniques and to follow the cutting-edge developments. Princehouse, 2003, p. 245.

growth of macroevolutionary Paleobiology has "moved paleontology from a marginal role compiling a photo album of the history of life on earth, to a central role as a source of evolutionary theory and of challenges towards further theory."[14]

Sepkoski's early career is a convenient lens to examine this shift for several reasons. First, because he was singled out by Gould for his potential to carry the torch for innovation in paleoecology; second, because he was later responsible for some of the field's major breakthroughs; third, because his papers, which have been recently made available following his death in 1999, contain an unusually complete record of the professional activities that he and his colleagues were engaged in the 1970s; and fourth, because by fortune or foresight, he happened to have exactly the right skills and interests in just the right place at right time when they would have a large impact on his field.[15] Sepkoski's activities in the 1970s serve as a case study and an exemplar of the emerging quantitative paleobiology, and help clarify Gould's strategy for bringing paleontology to the evolutionary high table.

Quantitative Pedagogy

When Sepkoski arrived at the Department of Geological Sciences at Harvard in 1970 he was already in possession of some fairly definite

[14] Princehouse, 2003, p. 6.

[15] Sepkoski, Jr. achieved notoriety for his involvement, during the mid-1980s, in the controversy surrounding the "Nemesis affair." He proposed, along with David Raup, the periodic cycle of mass extinctions at 26 million-year intervals, based on a large-scale statistical analysis of the marine fossil record. This study supported Walter and Louis Alvarez's discovery, at Gubbio, Italy, of an iridium band in the stratigraphic location between the Cretaceous–Tertiary boundary. This band was believed to be the deposit from a massive impact at the K-T boundary which killed the dinosaurs. Subsequently, a crater matching this age was discovered off the coast of the Yucitan Peninsula in Mexico, and several other putative craters have been linked to extinction events on the Sepkoski-Raup model. For detailed first-hand accounts of these events, see Raup, 1999 and Alvarez, 1997. Sepkoski spent most of his career in the Department of Geophysical Sciences at the University of Chicago, where colleagues included Raup and Thomas Schopf. He was the recipient of several major awards, including the Charles Schuchert Award from the Paleontological Society, and was elected as a foreign member to the Polish Academy of Sciences. He also took an active role in his profession, serving as editor for the journal *Paleobiology* from 1983 to 1986, and as president of the Paleontological Society in 1996. He died suddenly in his home in Chicago on May 1, 1999, of heart failure at the age of 50.

ideas about how he wanted to study paleontology.[16] At Notre Dame he had gotten a thorough education from Gutschick, chair of the Geology Department, in paleontology and stratigraphy, both from formal coursework and from independent research projects, field trips, and informal mentoring.[17] He was also interested, however, in applying statistical techniques to the final evaluation of data he had collected, and in the Fall of his senior year published a report on this work in the *Notre Dame Science Quarterly*. He was clearly encouraged by Gutschick to explore these areas, perhaps beginning during his junior year at Notre Dame in Gutschick's paleontology class. As a final project in that course, he conducted a statistical analysis of morphological differences in brachiopod samples, for which he plotted simple linear models correlating length, thickness, and width of the samples.[18] Examples of work from this early period also show, however, that Sepkoski was interested in developing new methods of computer analysis using more advanced statistical techniques. Shortly after receiving Gould's letter in 1971, Sepkoski revised a paper he had written at Notre Dame titled "Report on the Q-Mode Cluster Analysis Program for the Classification of Qualitative and Semi-Quantitative Data."[19] This was a technical study of a type of multivariate (cluster) analysis used to classify groups of samples from a data set according to the similarities between samples based on multiple variables, where Sepkoski presented a program (QMONON) written in FORTRAN to handle such problems.

There are a couple of important points to draw from this piece: First, it shows that Sepkoski was, while still an undergraduate, already capable of handling statistical programming which was – for its time – relatively sophisticated. He expressed surprise in a letter to Gutschick several years later that his undergraduate *Science Quarterly* article had

[16] It is worth noting that Sepkoski's dissertation was *not* a particularly quantitative or conceptual project: its title was "Stratigraphy and Paleoecology of Dresbachian (Upper Cambrian) Formations in Montana, Wyoming, and South Dakota," and his main advisor was not Gould but rather Bernhard Kummel. The dissertation had, however, very little to do with the trajectory of Sepkoski's career, either from an intellectual or a professional perspective. When he was hired at the University of Rochester in 1974 Sepkoski was nowhere near completion, and it was only several years later that he finally finished, mostly as a requirement for appointment at the University of Chicago in 1977.

[17] Sepkoski elaborates on his early experience in application essays he prepared for an NSF fellowship and for admission to Brown University. Sepkoski Papers, Box 2-1.

[18] Sepkoski, "Report on the Statistical Analysis of a Sample of the Brachiopods, Composita Sp., from the LaSalle Limestone (Pennsylvanian) Near LaSalle, Illinois," Sepkoski Papers, Box 25-1.

[19] Sepkoski Papers, Box 20-1.

been cited in a professional journal.[20] Second, the timing of the revision of the Q-Mode analysis program suggests he had taken Gould's advice seriously. Sepkoski notes that the program itself was revised in the Fall of 1970 (which would have presented evidence of his talents to Gould, who supervised the revision), but the report itself was not rewritten until June of 1971, approximately 2 months after he received Gould's letter. This timeline is borne out by a draft of a letter Sepkoski sent to Laporte at around the same time, in which he informed him of the decision to stay at Harvard because of "a number of considerations [which] have arisen which I was not regarding earlier."[21]

Sepkoski's coursework at Notre Dame included several classes in differential and integral calculus and an introductory computer science course, but only one semester of statistics – and a course on "management statistics" at that.[22] We should therefore infer that his training in this area was self-directed and/or conducted in private study with Gutschick, and was not part of any formal curriculum. When he began graduate school, then, he possessed a set of skills that was (a) unusual in a paleontology student, and (b) mostly self-taught. It was possible to add some formal coursework in these areas while at Harvard, although to do so required stepping outside of the traditional geology/paleontology sequence. In addition to further courses in statistics and mathematics, Sepkoski took courses in "Quantitative Methods," "Ecology," and "Applied Mathematics" – the latter two of which were taught by the mathematician William Bossert (whom Gould mentioned in his letter as a potential resource). Bossert is a particularly interesting influence: a member of Harvard's Engineering and Applied Science division, he had also done important work developing mathematical models for complex biological systems, such as evolutionary populations and modeling selection pressures.

The course on quantitative methods was probably the most significant introduction to current statistical trends in the field for Harvard paleontology graduate students. The course was taught by Gould and appears to have grown out of a seminar he offered his first year teaching at Harvard in 1968 titled, "Evolution and the Study of Ontogeny in

[20] Sepkoski to Gutschick, October 2, 1974. The article was "Silurian Reefs of Northern Indiana: Reef and Interreef Macrofaunas," by Robert H. Shaver, in the 1974 *AAPG Bulletin*.

[21] Undated draft of letter, Sepkoski to Laporte, 1971. This draft can be fairly definitively dated as having been written in May or June of 1971, because it is addressed to Laporte at Brown University, which he left later in the summer of 1971 to take a position at UC Santa Cruz.

[22] Sepkoski Papers, "Notre Dame transcript," Box 2-1.

Fossils." In the seminar Gould presented readings covering various aspects of the study of ontogeny, beginning with the 19th century approaches of D'Arcy Thompson and T.H. Huxley and ending with contemporary approaches using computer simulation and factor analysis, including papers by himself and Raup. The next year, Gould first offered his methods course, "Quantitative Methods in Paleontology," which guided students through many of the current approaches to quantitative methods in paleoecology.[23] Topics for the course included analysis of variance, matrix algebra, factor analysis, multiple regression and discriminant function analysis, multivariate numerical taxonomy, multivariate ontogeny and allometry, and multivariate study of phylogeny.[24] This course also reflected Gould's appreciation of the potential for quantitative analysis to enhance the status of paleontology: students were assigned Thomas Kuhn's article "The Function of Measurement in Modern Physical Science," which argues that the mathematization and quantification of a scientific discipline is an essential step towards making that discipline nomothetic.[25] Importantly, this seminar also required students to perform several projects using Wang programmable calculators and the SDS 940 computer, including a final project running data through a multivariate analysis program.

It appears, however, that Sepkoski's own independent review of the statistical literature was rapidly exceeding his teacher's expertise. Andrew Knoll recalls that when he took the course in 1974 it dealt mainly with factor analysis, and Sepkoski, acting as TA in his final year at Harvard, taught much of the class.[26] This corroborates Sepkoski's own recollection: in a letter several years later to Rebecca German, then a graduate student at Harvard, he "sympathize[s] entirely with your plight vis-à-vis Gould's multivariate course," which she was currently taking, remembering he "was in the identical situation when I took it my second year of graduate school – spent so much time trying [to] solve other students' computer problems (the TA couldn't), I had to take an incomplete." Nonetheless, he notes "things went much more smoothly the next time around, when I was the TA."[27] The fact that Gould offered the course at all demonstrates the importance he placed on

[23] For information on Gould's early teaching I thank Roger D.K. Thomas, who has generously provided insight and materials from this period. Thomas was an advanced graduate student when Gould first arrived at Harvard, and one of the first Harvard students to seriously pursue quantitative paleontology.

[24] Gould, Syllabus, "Seminar: Quantitative Methods in Paleontology," Spring 1969. Personal copy of Roger Thomas.

[25] Kuhn, 1961.

[26] Andrew M. Knoll, personal communication, July 14, 2003.

[27] Sepkoski to Rebecca German, January 10, 1980. Sepkoski Papers, Box 10-3.

quantitative techniques in the study of paleoecology – as will be discussed below – but it also reveals the limits to Gould's own personal expertise and sheds light on his reasons for encouraging his students to apply these methods to macroevolutionary problems. As another Harvard graduate student from the early 1970s recalls, "During its renaissance in the 1970s some paleontologists may have learned basic statistics from Steve Gould, but the gurus of the group for quantitative analysis and computer simulation of evolutionary processes were always Jack Sepkoski and David Raup."[28]

From Systematic Zoology to Paleobiology

While quantitative paleobiology was in its infancy during the late 1960s and early 1970s, many of its methods were adapted from the much more established techniques developed in the field of systematic biology during the preceding few decades. As Joel Hagen has shown, a "statistical frame of mind" emerged among biologists after World War II that took advantage of advances in computing technology which grew out of the post-war era.[29] In particular, two important books promoted quantitative techniques in this field: Simpson and Roe's *Quantitative Zoology*, which was first published in 1939 and later revised and updated by Richard Lewontin in 1960, and Robert Sokal and F. James Rohlf's *Biometry*, which appeared in 1969.[30] While Simpson's original volume was relatively simplistic by the standards of Sokal and Rohlf's far more exhaustive text, both works were extremely important for pointing the discipline in a more statistical direction and for demonstrating how quantitative analysis could help solve biological problems – such as population dynamics – that were too complex or had too many variables to study empirically. At the same time, journals like *Systematic Zoology* began to publish papers that were quantitative in orientation, making quantitative ideas in systematics accessible to a wider audience. Rohlf and Sokal first published a description of taxonomy using factor analysis in the journal in 1962, initiating a discussion concerning the use of computers and multivariate statistics that played out in the journal for the next 10 years.[31]

[28] Russell Lande, personal communication, July 15, 2003.
[29] Hagen, 2003.
[30] Simpson, Roe, and Lewontin, 1960; Sokal and Rohlf, 1969.
[31] Rohlf and Sokal, 1962. Other articles include Dice, 1952; Sneath, 1961; Sokal, Camin, Rohlf, and Sneath, 1965; Mayr, 1965; Rohlf and Fisher, 1968; Peters, 1968.

These publications had a significant effect on Sepkoski and other young paleontologists. A literature review compiled by Sepkoski between 1971 and 1974 contains detailed notes on books and articles by Sokal, Simpson, and John Imbrie (who wrote a short treatise on biometrical methods in 1956). In fact, Sepkoski's own first paper, "Distribution of Freshwater Mussels: Coastal Rivers as Biogeographic Islands," written with fellow graduate student Michael Rex, was published in *Systematic Zoology*.[32] This paper appeared in 1974 and is a study of the distribution of freshwater mussels. It makes use of a number of statistical techniques, including analysis of levels of association using Jaccard coefficients, stepwise multiple regression analysis, and Q-mode cluster analysis. Sepkoski and Rex note that in addition to using programs developed by other authors, they constructed "an independent stochastic model based on the processes of immigration along stepping stones," which had the advantage of "abstract[ing] from the real biogeographic system several factors known or thought to be important in influencing numbers of species."[33] As Michael Ruse has noted, this paper is particularly interesting because it takes the model of island biogeography developed by E.O. Wilson and R.H. MacArthur and turns it on its head: Sepkoski and Rex treat rivers as "islands in a sea of land," and interpret the pattern of distribution of mussels from one river to the next as analogous to the "stepping stone" distribution of land animals along an island chain.[34]

Sepkoski himself notes that he learned the theory of island biogeography directly from Wilson, who was his teacher in at least two biology courses at Harvard.[35] In fact, his graduate coursework was heavily biological: his notebooks record classes taken on Evolution & Behavior (with Wilson), Ecology (with Bossert), Biogeography (also with Wilson), Species Diversity, and Principles of Evolutionary Biology (a team-taught course whose faculty included Ernst Mayr).[36] The importance of this coursework to Sepkoski's intellectual development cannot be overstated: at Notre Dame he did not take a single biology course, so his classes at Harvard constituted his first systematic exposure to the subject.[37] Wilson and MacArthur's book on island

[32] The literature review comprises two notebooks in the Sepkoski Papers, Box 24-5. The paper is Sepkoski and Rex, 1974.

[33] Sepkoski and Rex, 1974, p. 175.

[34] Ruse, 1999b, p. 215.

[35] Sepkoski, 1994, p. 133.

[36] Sepkoski Papers, Boxes 25-2 and 25-4.

[37] Sepkoski Papers, "University of Notre Dame Transcript." Ruse (1999b) also makes this point.

biogeography may have been the impetus for the 1974 paper (it was the assigned text for Sepkoski's Biogeography course), but it appears that Wilson's textbook *A Primer of Population Biology*, which he co-authored with Bossert, had a deeper lasting influence. This book grew out of an unpublished primer the two professors had used for several years in their introductory evolutionary biology course at Harvard, and presented itself as an introduction to mathematical and quantitative methods for aspiring biologists.[38] In its introduction, the authors argued that progress in evolutionary biology is impossible without analytical techniques, and they cited William Thompson's (Lord Kelvin) famous dictum "unless you have measured it, you don't know what you are talking about." "Measurement," according to Wilson and Bossert, means "mathematical model building, measurement techniques, and problem solving," and they warn "where such quantitative refinements do not exist, their invention stands as a challenge to theoretical biologists."[39]

Sepkoski's real interest in biogeography lay, however, not in neontologic distribution, but rather in extending this model to rates of speciation and extinction in the fossil record. As Ruse puts it, "if one thinks of the future (now a past-future to us) as a space to be colonized, what interplay would one expect, given certain specified rates of species innovation (corresponding to species arriving on islands) and of extinction (corresponding to species leaving or being wiped out from islands)?"[40] Wilson and MacArthur's work predicts that initial growth in island populations will be followed by equilibrium, as selection pressures mount and balance out "arrivals" (or speciation) with "departures" (or extinctions). Sepkoski's work over the next several years, from 1975 to 1979, dealt with these questions, and ultimately produced an answer that in a general sense confirmed the prediction of the MacArthur–Wilson model for Paleozoic communities. The summation of this work is presented in three articles published in *Paleobiology*, which purported to present a "kinetic model" of Phanerozioc taxonomic diversity.[41] The aim, as Sepkoski relates it, is to "describe interrelationships among a small number of variables" such as speciation, extinction, and taxonomic diversity, "and show how these should vary with respect to one another and to time."[42]

[38] Wilson and Bossert, 1971, p. 10.
[39] Wilson and Bossert, 1971, p. 9.
[40] Ruse, 1999b, p. 215.
[41] Sepkoski, 1978 and 1979.
[42] Sepkoski, 1978, p. 223.

The analysis in these papers draws heavily on the "logistic equation" developed in population biology (which had significant emphasis in Wilson and Bossert's *Primer*). Briefly, the logistic equation is a well-established model for characterizing the growth of populations over time as a function of birth rates, death rates, and environmental constraints on intrinsic growth. Birth and death rates are assumed to have a reciprocal relationship – as population growth exceeds deaths and approaches the sustainable limit of the environment, the model predicts that birth rates will level off. A standard form of this equation is $\frac{\Delta N}{\Delta t} = rN\left(\frac{K-N}{K}\right)$ where $\mathbf{\Delta N}$ is change in number of individuals (either increase or decrease), $\mathbf{\Delta t}$ is change in time, **r** is the "intrinsic rate of increase" (also known as the 'Malthusian parameter'), and **K** is the population limit.[43] This equation yields the following logistic growth curve (Figure 1). Note that the shape of the curve is sigmoidal; after an initial burst in growth, the population levels off as it approaches its limit, or the "carrying capacity" of the environment. Growth curves can also be negative, which indicates a population destined for extinction.

The logistic equation was initially formulated in 1920 by the biologist Raymond Pearl and his associate Lowell J. Reed to explain demographic trends in the United States. As Sharon Kingsland has shown, this model was quickly adopted by population biologists in the 1930s and 1940s, who adapted it "as a tool of research… a logical argument which expressed how a population might grow if certain initial conditions were met."[44] Particular supporters were Alfred James Lotka, who studied with Pearl while preparing his *Elements of*

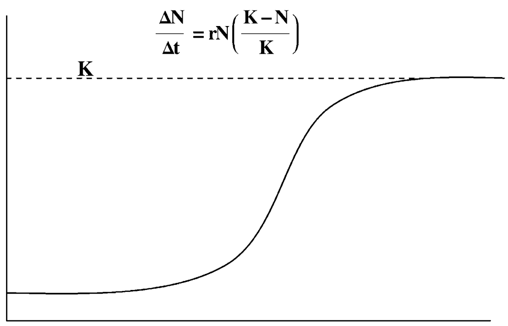

Figure 1. Logistic Growth Curve (After Wilson and Bossert, 1971).

[43] Wilson and Bossert, 1971, pp. 16–19, 92–106.
[44] Kingsland, 1982, pp. 40–41.

Physical Biology (1925), and Georgii Frantsevich Gause, who published the influential book *The Struggle for Existence* (1934).[45] Over the next several decades the model became firmly established as a standard tool in population biology and ecology, and played a significant role in the movement towards quantification in those disciplines. Indeed, as Kingsland notes, MacArthur and Wilson, who adapted the logistic equation to island biogeography, hoped such methods would "galvanize biogeography and have extensive repercussions in ecology and evolutionary theory," and promote a more "experimental and theoretical phase" in the field.[46]

It is difficult to pinpoint exactly how the logistic equation made the translation from biology to paleontology, but Sepkoski unquestionably had a major role in the process. Since his first exposure to population biology and ecology came in courses with Wilson and Bossert, it seems likely that the *Primer* was his initial point of entry. Nonetheless, in the bibliographies for the first two kinetic model papers (1978 and 1979), he cites a number of important sources: Robert May's monograph on model ecosystems, Daniel Simberloff's essay on biogeographical models, Steven Stanley's paper in *Quantitative Zoology* on competition rates in evolution, and Gause's *Struggle for Existence*.[47] While all of these works make some form of reference to the logistic model, Sepkoski's use of the sigmoidal growth curve was the most explicit. His kinetic model papers transpose the equation from living populations to phylogenies in the fossil record, substituting originations and disappearances from the fossil record for the predator–prey relations between individuals (i.e. the Lotka–Volterra equations) or the arrivals and "departures" (or extinctions) of the island biogeographical model.

Here Sepkoski treated entire taxa as analogous to individuals, and reasoned that they were subjected to the same population pressures. As he wrote several years later, the historical pattern of clade diversity is "topographically identical" to biological population growth.[48] The three papers published between 1978 and 1984 examined the rates of per taxon diversification and extinction, and plotted them over a large portion of geologic time (Figure 2). He found that the actual rates of speciation and extinction for marine fauna matched those predicted by

45 Kingsland, 1982, p. 30 and 41; see also Kingsland, 1985, chapter 4.
46 Kingsland, 1984, p. 192. See MacArthur and Wilson, 1963 and 1967.
47 May, 1973; Simberloff, 1972; Stanley, 1973; and Gause, 1934.
48 Sepkoski, 1991, p. 136.

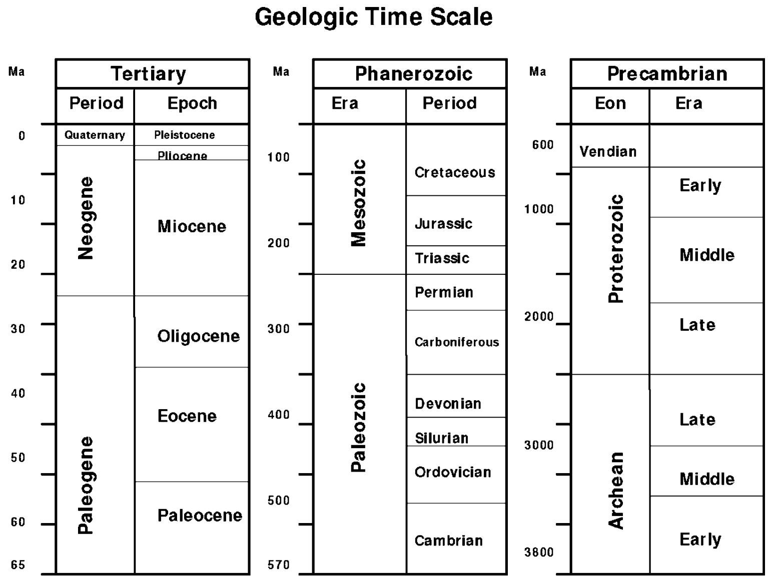

Figure 2. Geologic timescale.

the mathematical model, suggesting a macroevolutionary pattern in the Phanerozoic that could be expressed as a series of three logistic curves.[49] (Figure 3) These individual curves each represented a distinct evolutionary fauna: one for the Vendian–Cambrian, one for the

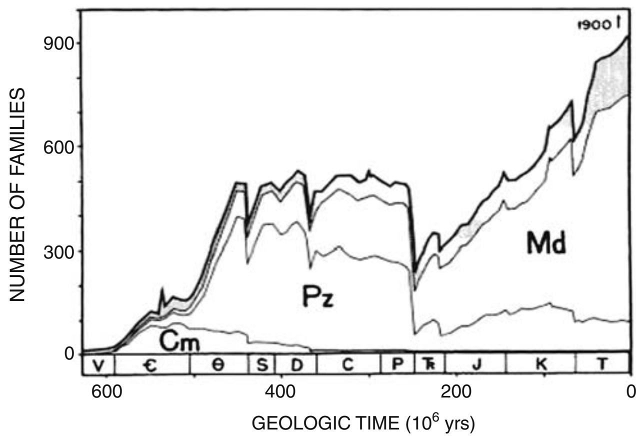

Figure 3. Logistic graph of Phanerozoic faunal replacement (from Sepkoski, 1984, p. 249).

[49] See Sepkoski, 1979, pp. 245–246 and Sepkoski, 1984, pp. 264–265.

post-Cambrian Paleozoic, and one for the Mezozoic–Cenozoic periods. Sepkoski concluded that "each evolutionary fauna can be approximated by a simple logistic function," exhibiting a characteristic burst of speciation initially, followed by a long period of equilibrium, and ultimately (except for the last stage, which is ongoing) a decline.[50]

Quantitative Paleobiology as Collaborative Enterprise

This work was not done in isolation. An earlier study conducted by Gould, Raup, Schopf, and Simberloff attempted to simulate the evolution of diversity using stochastic (or random) simulations of phylogeny. In a paper published in 1973 in *Journal of Geology*, the group reported on the efforts to generate random phylogenetic trees (using a computer program) to test whether these would replicate certain aspects of actual phylogenies – thus demonstrating whether actual patterns of origination and extinction had stochastic variables.[51]

The genesis of this paper was an informal meeting in late 1972 at Woods Hole that included Schopf, Raup, Simberloff, and Gould. As Princehouse reports, Schopf was the instigator: he had decided that paleontology required new methodologies, and he targeted the others as exciting young contributors to the field.[52] Sepkoski was included in the discussion, meeting with the others for the last day.[53] According to Gould, Schopf had a grand vision for the discipline: "he yearned to convert an empirical field, manifestly short of ideas to unite its fascinating particulars, into a science based on experiment, construction of null hypotheses, rigorous test… To rescue paleontology, convert it to an exciting "chancy young man's game" (a phrase from E.O. Wilson that he particularly liked)." Schopf's ambition was no less than to discover a set of "gas laws" for paleontology that would reveal the "timeless regularities" of the laws of evolution.[54] The Woods Hole meeting, then, was his first step towards making this vision a reality. The second was to establish, against the better judgment of much of the paleontological community (including Raup), to found and edit the journal *Paleobiology*.[55]

[50] Sepkoski, 1984, p. 265.
[51] See Raup et al., 1973.
[52] Princehouse, 2003, pp. 204–215.
[53] Though he was not listed as a co-author on the 1974 paper, he was included in a follow-up study published in 1977 by the same group. See Gould, Raup, Sepkoski, Schopf, and Simberloff, 1977.
[54] Gould, 1984, p. 280.
[55] Schopf served as editor of *Paleobiology* until 1980. Sepkoski took over the editorship between 1983 and 1986.

Raup recalls that the most significant result of the meeting was to settle on macroevolution as the phenomenon to study. According to Raup,

> We all had basic population genetics but it was difficult to know how to apply that… [W]e all had high hopes for the direct application of population genetics to the fossil record and several attempts had been made and we hadn't come up with much and so I think we were looking for macroevolution. We were looking for something at a higher level which would have been more accessible with the kind of data we had. I don't think the word macroevolution was used, but I think that's what we were struggling for.[56]

Gould in particular was interested in testing his intuition that there were patterns to the fluctuations in diversity observed over geologic time. This led to a follow-up study, with Raup, in which the authors ran an extensive computer simulation of hypothetical phylogenies, this time including an important new variable to their simulation: randomly changing morphology. This paper, published in 1974 in *Systematic Zoology*, argued that stochastic modeling shows the common paleontological assumption that evolution of morphology is the result of uni-directional selection to be problematic. Specifically, the authors ask "whether random change in morphology in a phyletic context can yield evolutionary order – and to comment on what that order means, if it exists."[57]

This is one of the first publications to use statistical computer modeling to explicitly call conventional evolutionary theory into question. The authors note that any larger claims they make must be taken with caution: their model can be interpreted as consistent with Darwinian selection if morphological changes are interpreted as phenotypic variations adapted to random changes in environment, or with non-Darwinian mechanisms like genetic drift, if the changes are seen as random mutations. What the model does not support, however, is the superimposition of directional causes onto evolutionary phylogeny. If their randomly generated phylogenies show "a familiar evolutionary order" (which they do), then "an ordered pattern of morphological change through time supplies no proof for uni-directional selection if the pattern can be generated by random processes as well."[58] The assumption in evolutionary systematics is that the similarity of taxa

[56] Raup, quoted in Princehouse, 2003, pp. 211–212.
[57] Raup and Gould, 1974, p. 306.
[58] Raup and Gould, 1974, p. 306.

within a given clade is a reflection of the recentness of their common ancestry. If this were true, randomly-generated phylogenies "would not display this essential property of morphologic coherence within clades," thus supporting the idea that coherence and order in actual phylogenetic trees is maintained by "stabilizing selection." Raup and Gould found, however, that "the randomly changing morphology of our evolutionary trees displays the same property of coherence" as those drawn from nature, meaning that the "order" observed in phylogeny *can* (but not necessarily *must*) be a product of random factors.[59]

Beyond the significance of this challenge to received evolutionary theory, this argument is notable for its methodology: here, the computer program is not just a tool for statistically sorting empirical evidence; rather, it is part of the evidence itself. This relates to a larger methodological agenda of the authors, reflected in a statement cleverly snuck into the acknowledgments at the end of the paper. Raup and Gould credit the members of their earlier study – Schopf and Simberloff – and note that they all are

> motivated by a common conviction that paleontology could use the insights of modern population ecology to become a more nomothetic discipline. We know of no other field that has been so persistently idiographic in its methodology – concentrating, when it seeks to explain at all, on the explanation of particular events at particular times. We are convinced that sequences of unique historical events have strong general components (regulated by laws that are independent of time, space and taxonomic group) – and that it is the (heretofore neglected) task of paleontology to discover them (not by induction from empirical catalogues, but by attempts to model results with comparatively simple systems).[60]

This, in a phrase, is the "great innovation" Gould was hinting at in his letter to Sepkoski, and three years after that letter was written Gould had actively drawn Sepkoski into the project.

Sepkoski had been involved all along with this study, in particular by supplying his computer expertise to the project by writing the program (COLINK) used in the stochastic simulations. In order for the findings of the simulation to be more than simply an intriguing hypothesis, however, the patterns found in the hypothetical phylogenies needed to be correlated with actual evolutionary lineages. For this task, Gould hired Sepkoski to collect as much data on actual taxa as he could –

[59] Raup and Gould, 1974, p. 308.
[60] Raup and Gould, 1974, pp. 321–322.

orders, families, and genera – from existing compendia of the fossil record, such as Harland et al.'s *Fossil Record* and Moore et al.'s *Treatise on Invertebrate Paleontology*. Sepkoski was working on his dissertation at the time, and had some insights into how the record might be improved by adding greater precision to stratigraphic assignments of fossils.[61] This project ultimately ballooned into Sepkoski's massive *Compendium of Fossil Marine Families*, which was first published in 1982 and has been continually updated by Sepkoski and others to the present day.[62]

Despite the fact that this project was not yet complete, by 1978 Sepkoski had gathered enough data to form some conclusions about the relationship between the simulated models and the actual record. In his 1978 paper on the kinetic model of Phanerozoic diversity, Sepkoski wrote that the simulations predict "specific quantitative patterns in taxonomic diversity and in relative magnitudes of origination and extinction rates that can be tested statistically with paleontological data."[63] The conclusions of that paper were that the logistic model, which predicted a semi-sigmoidal rise in diversity followed by a fluctuation around an equilibrium, was borne out by analysis of the actual marine metazoan record – based in part on Sepkoski's new fossil data.[64] The resulting picture was of a slow, steady rise in diversity beginning in the late Vendian, reaching a peak in the mid-Ordovician, followed by a steady state of equilibrium. (Figure 4). This is precisely what the com-

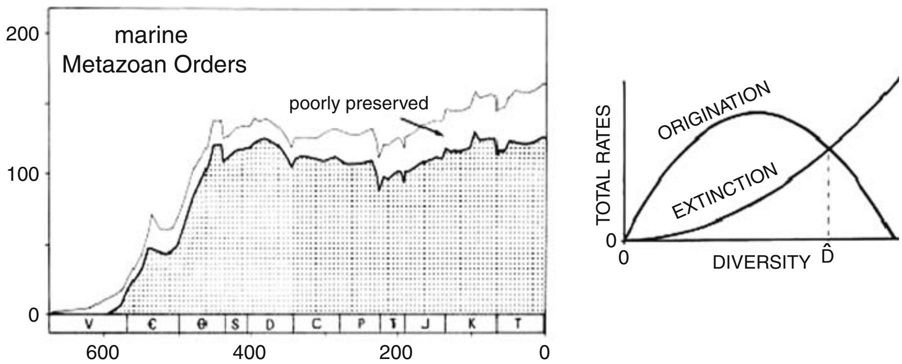

Figure 4. Single-curve growth model (From Sepkoski, 1978, p. 234).

[61] Sepkoski, 1994, p. 135.
[62] Sepkoski, 1982. The most current edition is available as a CD-Rom from the Paleontological Research Institution.
[63] Sepkoski, 1978, p. 224.
[64] Sepkoski, 1978, pp. 244–245.

puter simulation predicted: when models for origination and extinction are superimposed, a point of equilibrium is reached that corresponds to the intersection of the two curves.

At the end of the paper, Sepkoski notes that his model "is not a complete causative account of the history of life but rather a description of the fundamental patterns in the temporal behavior of taxonomic diversity."[65] Indeed, he quickly realized that the model had a major fault: based, as it was, on the level of orders, it obscured a more subtle pattern that was revealed by modeling data collected on diversity at the level of families. When examined at the familial level, the curve plotted for families with late Proterozoic originations reaches a kind of "pseudo-equilibrium" in the mid-Cambrian, and then heads into a steady decline. At the same time, a new group of families, which Sepkoski termed "Paleozoic fauna," began to rise, reaching an equilibrium in the mid-Ordovician with "three times the familial diversity" of the first curve. This led to the second paper, in 1979, that corrected this by plotting a new sequence which referred to a "two-phase" kinetic model of diversity, in which the rise, equilibrium, and decline of the Cambrian fauna was overlapped by a similar pattern in later, Paleozoic fauna (Figure 5)[66] However, the argument was not yet quite complete. Further refinement in the data showed that the Paleozoic fauna, like that of the Cambrian, also reached a point of decline after a stage of equilibrium, and gradually petered out between the Permian and Triassic periods. At

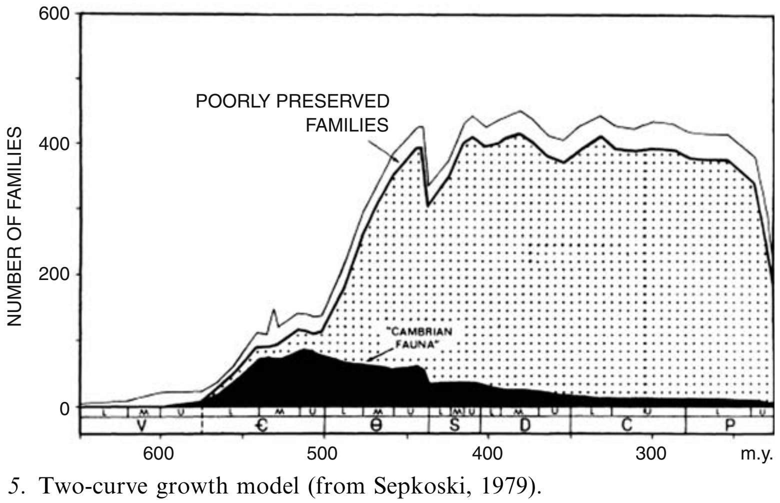

Figure 5. Two-curve growth model (from Sepkoski, 1979).

[65] Sepkoski, 1978, p. 245.
[66] Sepkoski, 1979.

the same time, though, a new faunal expansion could be observed rising to replace the Paleozoic group, which has continued to rise in diversity up to the modern day. In the third paper, published in 1984, Sepkoski presented his "three-phase kinetic model," which plots the overall patterns in Phanerozoic diversity as a series of three, overlapping diversity curves (see Figure 3).[67]

Towards a Nomothetic Paleontology

Sepkoski's analysis presented a striking implication for broad macroevolutionary patterns: it did not conform to the gradual model expected if either adaptations in classic Darwinian natural selection or genetic accumulations in the Modern Synthesis are the sole mechanisms for evolutionary change. The apparent tendency for taxa to rise, level out, and decline *en masse* suggests that in addition to microevolutionary adaptive factors, a broader evolutionary mechanism operates at the level of families and perhaps species. This raises the possibility – promoted by Gould and Eldredge – of species selection as a major factor in evolution.[68] In his first "kinetic model" paper Sepkoski seems to have been aware of this connection, and he openly acknowledged the methodological path that made these conclusions possible. He writes

> Models of paleontological diversity can be constructed with forms analogous to those of classic population ecology. Eldredge and Gould (1972), Stanley (1975), and Gould and Eldredge (1977) have forcefully argued that the majority of species, like individuals, are discrete and fairly static entities with constant or mildly varying morphologies and ecologies throughout most of their durations. Origination and extinction probably involve periods of time that are relatively short compared to the total durations of the species. If we assume with proper caution that these properties make species analogous to individuals, an entire suite of conceptual and mathematical models of population dynamics becomes available for prudent use in studies of cladogenesis.[69]

[67] Sepkoski, 1984.

[68] Species selection, and the related idea of group selection, were relatively underdeveloped concepts at the time, but scientists clearly had an intuition that some process was being observed at the species level which was analogous to change at the individual level. For a more detailed analysis of these concepts, see Gould, 2002, pp. 646–652.

[69] Sepkoski, 1978, p. 224.

This is precisely the approach to reconstructing the methods and goals of paleontology that Gould was hinting at in his letter to Sepkoski of 1971, and it represents a kind of empirical verification of the intuition Gould and Eldredge promoted in their theory of punctuated equilibria.

In 1980, Schopf – still editor of *Paleobiology* – asked Gould to contribute several articles assessing the "Status of Paleontology – 1980." Gould happily obliged, and in a single issue of the journal published two reflective essays on the state of the discipline. In the first, which he titled "The Promise of Paleobiology as a Nomothetic, Evolutionary Discipline," Gould both celebrated the recent advances in paleontology and reiterated his call for further progress towards revision of evolutionary theory based on macroevolutionary modeling. One of Gould's overarching concerns was to raise the status of paleontology with respect to other evolutionary fields, and he was now pleased to report that "our profession now wears the glass slipper and, if not queen of the evolutionary ball, at least cuts a figure worth more than a passing glance."[70] One of the factors Gould cites in this development directly recalls the advice he gave Sepkoski to transfer the insights of other disciplines to paleontology: advances had been made over the past 10 years (Gould uses 1969 as a starting point) because "new ideas arise more often by the creative juxtaposition of concepts from other disciplines (as in Darwin's case) than from the gathering of new information within an accepted framework."[71] The most significant direction the discipline has taken has seen "Simpson's procedure of modeling and testing" gaining widespread acceptance, and the reduction of emphasis on ideographic studies in the "'empirical law' tradition."[72]

Among the examples of the new, nomothetic approach Gould cites is Sepkoski's study of Phanerozoic diversity, which Gould lauds for combining the traditional orientation of the discipline with the new. Of Sepkoski's "two-curve" model (the third curve was of course added several years later), Gould writes

> Here we see an interesting and fruitful interaction of nomothetics and ideographics. The form of the model remains nomothetic – the "real" pattern arises as an interaction between two general curves of the same form, but with different parameters. Ideographic fac-

[70] Gould, 1980, p. 96.

[71] Gould, 1980, p. 97.

[72] In this sense, the term "ideographic" refers to information which is presented in a pictoral or figurative manner.

> tors determine the parameters and these enter as boundary conditions into a nomothetic model.[73]

This, in Gould's estimation, represents the best potential for paleontology, which "resides in the middle of a continuum stretching from ideographic to nomothetic disciplines," and the discipline should certainly not lose sight of its "body of ideographic data virtually unparalleled in interest and importance among the sciences – for it is, after all, the history of life." Nonetheless, he sees evolutionary theory as "the center of a nomothetic paleontology," and furthermore the specific sub-discipline of paleobiology as "the locus of its construction."[74] Sepkoski's work was a potential example of such law-producing science because it applied a deductive model (e.g., the logistic equation) to a large body of statistically relevant empirical evidence, and offered the possibility for establishing general, predictive claims about patterns in macroevolution.

The letter from Gould to Sepkoski which began this essay, then, serves as a lens through which we can examine several important factors in the transformation of methods and goals in paleontology during the 1970s. It certainly initiated the successful career of an individual paleontologist, for whom it clearly provided guidance at a crucial time. One particular piece of advice the letter offered was to pursue deductive models from other disciplines, and we have seen how Sepkoski actively mined resources at Harvard and elsewhere to pursue this goal. Gould's letter also suggested that Sepkoski had skills that made him a particularly good candidate for this kind of interdisciplinary work, and here we can view Sepkoski's early career as a case study in the emergence of a new kind of paleontologist – one whose abilities in mathematics and computer programming were as important as more traditional areas like stratigraphy and systematics.

I note that Gould's intentions in his letter were not, however, purely altruistic. In 1971 Gould was on the verge of presenting his work with Eldredge on punctuated equilibria to the world, and he knew that he would need substantial support over the next years to establish both the empirical veracity of this model and the kind of deductive approach used to construct it.[75] Having spotted Sepkoski's talents in his quantitative methods seminar the previous fall, Gould used a light touch – he opened the letter with the comment that "your decision includes (apart from its truly intellectual proportions) so many emotional factors that I

[73] Gould, 1980, p. 115.
[74] Gould, 1980, p. 116.
[75] Eldredge and Gould, 1972.

can neither assess or weigh" – as well as some not-so-subtle flattery to make sure he kept Sepkoski in the fold. Having accomplished this, he immediately engaged Sepkoski in the exciting work he was pursuing with Raup, Schopf, and others, ensuring that his student would both benefit from exposure to the best minds in the field and also immediately begin contributing to the project. From this story emerges another facet of Gould's professional persona that is less often recognized – that of inspiring teacher and skillful pedagogical strategist. Despite having a very limited effective tenure as an active member in his department at Harvard, Gould trained a number of PhDs in paleontology, biology, and history of science.[76] Many of those students – like Sepkoski – went on to train their own students in the quantitative and "nomothetic" approach to paleontology, further cementing Gould's impact on the field. This impact has been substantial: while punctuated equilibrium has had a bumpy reception over the years, his more general agenda for challenging received wisdom about the tempo and mode of evolution, questioning Darwinian adaptationism as a primary mechanism for speciation, and raising the status and scope of paleontology has fared much better.[77] Gould was certainly not shy about making bold claims for himself and his field, nor was he afraid to make predictions about its future direction. In his letter to Sepkoski in 1971 he did just that and, in ways both large and small, his predictions proved correct.

Acknowledgments

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[76] Allmon, 2002, p. 938.

[77] Despite its initial reception, the jury still seems to be out on punctuated equilibria, judging from the remarks of several of Gould's eulogists and the passionate defense Gould gave the theory in *The Structure of Evolutionary Theory*. Gould, 2002.

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