“Towards a Nomothetic Paleontology”: The MBL Model and Stochastic Paleontology

The Roots of Nomotheticism

By the early 1970s, the paleobiology movement had begun to acquire considerable momentum. A number of paleobiologists began actively building programs of paleobiological research and teaching at major universities—Stephen Jay Gould at Harvard, Tom Schopf at the University of Chicago, David Raup at the University of Rochester, James Valentine at UC Davis, Steven Stanley at Johns Hopkins—which would flourish as centers of the movement over the next decade. Schopf had organized a well-received book (Models in Paleobiology) that presented exciting new theoretical approaches to the study of fossils. The movement even had its own textbook—Principles of Paleontology, published in 1971 by Raup and Stanley—that would provide an essential pedagogical foundation for paleobiology for the next two decades. And the establishment, in 1975, of the journal Paleobiology ensured that the “new paleobiology” would have a friendly outlet for publication and a platform from which to promote its agenda.

Nonetheless, not all of the elements of a paleobiological revolution were yet in place. While punctuated equilibria would eventually acquire iconic status as one of the movement’s signature theories, there was as yet no central theoretical and methodological commitment among paleobiologists. Paleobiologists could agree on some basic tenets: that the fossil record provided genuine insight into evolutionary rates and processes, that quantitative analysis and modeling using computers promised exciting new avenues for research, that insights from biology and ecology could more profitably be applied to paleontology, and that the future lay in assembling large databases as a foundation for analysis of broad-scale patterns of evolution over geological history. But in comparison to other expanding young disciplines—like theoretical ecology—paleobiology lacked a cohesive theoretical and methodological agenda. However, over the next ten years this would change dramatically.

One particular ecological/evolutionary issue emerged as the central unifying problem for paleobiology: the study and modeling of the history of diversity over time. This, in turn, motivated a methodological question: how reliable is the fossil record, and how can that reliability be tested? These problems became the core of analytical paleobiology, and represented a continuation and a consolidation of the themes we have examined thus far in the history of paleobiology. Ultimately, this focus led paleobiologists to groundbreaking quantitative studies of the interplay of rates of origination and extinction of taxa through time, the role of background and mass extinctions in the history of life, the survivorship of individual taxa, and the modeling of historical patterns of diversity. These questions became the central components of an emerging paleobiological theory of macroevolution, and by the mid 1980s formed the basis for paleobiologists’ claim to a seat at the “high table” of evolutionary theory.

This chapter will explore the beginnings of this development in paleobiology by examining the emergence of a new, clearly-articulated agenda: the often-expressed desire to construct a “nomothetic paleontology.” This phrase originated in 1973 in the first of an important sequence of papers that sought to develop a stochastic, equilibrial simulation of evolutionary dynamics over time—what came to be known as the MBL model—and quickly became a rallying cry (most often repeated by Gould, its inventor) for the new approach to paleobiology. The term “nomothetic” essentially means “law-producing,” and John Huss has outlined some of the essential features of this approach:

“Nomothetic” paleontology would: (1) work from the top down, deducing consequences from general models (i.e., models applicable across times and taxa); (2) predict the behavior of evolutionary events as statistical ensembles, rather than individually, (3) use equilibrium models as comparative baselines to single out elements requiring explanation in terms of specific, non-
recurring causes; and (4) attempt to replicate empirical phenomena using the minimum necessary departure from a simple random model (Huss 2004, 53).

This goal would manifest itself in a number of ways throughout the period that will be considered in this and succeeding chapters, and while its ultimate accomplishment may have been elusive, it nonetheless both helped focus paleobiologists towards a set of more achievable aims, and also gave the movement a greater sense of purpose.

The 1970s also saw a decade of debates among a core group of paleobiologists that illuminate some of the central themes and tensions in the new paleobiology. These themes encompass some of the basic methodological and philosophical issues confronting paleobiology, which ultimately resolve to between distinct and competing interpretations (or metaphors) for how best to “read” the fossil record, which entailed divergent responses to how to solve “Darwin’s dilemma” for paleontology.

Darwin himself recognized that if the fossil record were to be taken at face value—or “read literally”—it would challenge many of his assumptions about the tempo and mode of the evolutionary process. However, a small but influential group of paleontologists, from John Phillips to George Gaylord Simpson, argued forcefully that the fossil record was a less imperfect document that Darwin had suspected. It was precisely on this basis that Eldredge and Gould’s 1972 paper on punctuated equilibria endorsed a more prominent role for paleontology:

Many breaks in the fossil record are real; they express the way in which evolution occurs, not the fragments of an imperfect record. The sharp break in a local column accurately records what happened in that area through time. Acceptance of this point would release us from a self-imposed status of inferiority among the evolutionary sciences. Our collective gut-reaction leads us to view almost any anomaly as an artifact imposed by our collective millstone—an imperfect fossil record (Eldredge and Gould 1972, 96).

From the earliest drafts onward, Eldredge and Gould invoked the metaphor of “reading,” calling for “a more literal interpretation of the fossil record” or, as elsewhere stated, “the concept that phylogeny can be read directly from the rocks” (Eldredge, draft 1, 14 and 17; Eldredge pap.). However, developments to be discussed over the next two chapters would introduce an alternative, approach in which the fossil record was not to be read literally, but rather idealized, abstracted, and generalized from. In various ways, paleobiologists attempted to use analytical techniques to identify and circumvent limitations in the fossil record, a document they acknowledged could never be “read literally.” Almost from the very start, then, the revolutionary phase of paleobiology endorsed two, potentially conflicting metaphors for re-reading the fossil record: a “literal” versus an “idealized” approach (to complicate matters even further, Gould was involved as a primary advocate of both interpretations).

Reconciling these two metaphors was a central obstacle for the success of the paleobiological movement. I will argue in the next chapter that the emergence of a “taxic approach” to paleobiology in the late 1970s brought a partial reconciliation of these two metaphors, though lingering disagreements still remained.

**Reading as Idealization: The MBL Model and “Stochastic Paleontology”**

**The Origin of the MBL Project**

The simulation project that came to be widely known in the paleobiological community as the MBL model was the result of a collaboration, instigated by Tom Schopf in 1972, between Schopf, Gould, Raup, and Dan Simberloff, who met informally for discussions at the Marine Biological Laboratory in Woods Hole (hence the name MBL). The model itself was presented in a series of jointly authored papers between 1973 and 1977, after which point the collaboration effectively disintegrated.

In its most basic terms, the MBL model was a computer simulation of the evolution of hypothetical, randomly-generated lineages or “phylogenies” that tested whether random phylogenetic patterns could be produced that matched actual patterns in the fossil record. The general idea was that these simulations provided a null hypothesis against which the assumption that evolutionary patterns are deterministic could be tested; more broadly, this can be seen as part of paleobiologists’ efforts to determine whether the fossil record is a reliable document. As with the Models project and the launching of Paleobiology, Schopf’s participation was formative and essential. However, whereas Schopf’s role in those other endeavors was primarily organizational and administrative, in the MBL project Schopf made an important creative and theoretical contribution. Indeed, Schopf would come to regard the MBL model as his primary in-
tellectual contribution to paleobiology, and identified it very closely with his grand personal vision to build a “stochastic” or “particle paleontology” (Schopf’s term) in which the history of life could be idealized as a series of “gas laws.” Schopf’s energy and enthusiasm for this vision initially bound the group together and inspired its successes; as time went on, however, it also became a source of internal discord that ultimately led to the collaboration’s dissolution.

Like many of the major events in the growth of paleobiology, chance and contingency played significant roles in the origin of the MBL model. In early 1972, even as the Models volume was being finalized, Schopf was looking ahead to the next opportunity to advance the agenda of paleobiology. As discussed in chapter 6, he had already begun to explore the possibility of starting a new journal. But he also wanted to capitalize on the intellectual momentum of the Models symposium and book. Schopf usually spent his summers at Woods Hole, and in 1972 Gould was also planning to spend time there working on the draft of what would eventually become his first book, Ontogeny and Phylogeny (Schopf to Gould, 3 February 1972: Schopf pap. 5, 14; Gould 1977). Schopf decided to take advantage of this coincidence by organizing a small brainstorming session involving Raup and Simberloff as well. He described the meeting in his invitation to Raup as an opportunity “to get together for about 3 days to discuss the way in which theory can be more directly introduced into invertebrate paleontology.” Clearly, Schopf envisioned the session as an explicit continuation of the Models project, although there is little indication he had any distinct ideas about what form the collaboration might take. As he continued in his letter to Raup,

Of course, one can never “program” good research, and in any event research is always done by individuals and not teams, yet the self-conscious attempt to introduce more theory into our mass of facts might be a very useful thing to do. I have heard about similar affairs working out well; perhaps the most spectacular were the various outcomes when Lewontin, Ed Wilson, McArthur [sic], Levins and Egbert Leigh met for a week or so over a couple of summers at McArthur’s [sic] New Hampshire farm in the early ’60’s (Schopf to Raup, 5 March 1972: Schopf pap. 3, 30).

At first blush it might seem odd that Simberloff—a newly minted PhD in ecology with very little experience in paleontology—would be included in this group. Schopf’s only previous interaction with Simberloff had been in producing the Models volume, where Simberloff had, after all, been a second-choice replacement for E. O. Wilson. It appears, however, that from the very start Schopf imagined that equilibrial island biogeography would have a prominent place in the brainstorming sessions, and in that light Simberloff was a natural choice. Not only had he trained with Wilson, but as Schopf went on to explain, “Simberloff has the mathematical tools which might be required, is hungry to advance a field different from his dissertation area, and during a 2–3 hour conversation over dinner [at the GSA meeting in 1971] appeared to be a very perceptive, responsible and reasonable fellow” (Schopf to Raup, 5 March 1972: Schopf pap. 3, 30).

In retrospect, MacArthur and Wilson’s theory of island biogeography had a formative influence on inspiring paleobiology to become more models-oriented. Schopf was a central conduit for this influence. He had come to know Wilson casually during summers spent at Woods Hole, and the two developed a cordial relationship. When, for example, several years later Wilson became embroiled in his infamous controversy over sociobiology with Gould, Lewontin, and others, Schopf wrote Wilson to express his “greatest personal sympathy” and “great deal of affection” for Wilson. He also noted, “You have been of great help to me at Woods Hole, and I have, as you know, a very high regard for you scientifically, and to the extent that I know you and your family, also personally” (Schopf to Wilson, 2 March 1976: Schopf pap. 5, 35). Wilson wrote back to thank Schopf and to “reciprocate the feelings of friendship that motivated it” (Wilson to Schopf, 4 March 1976: Schopf pap. 5, 35).

Schopf’s friendship and admiration for Wilson had a significant intellectual effect on Schopf, and from fairly early in his career Schopf gave serious consideration to Wilson’s equilibrium model. In an autobiographical sketch written in 1976, Schopf noted that his first use of equilibrium models was in a paper that was “helpfully reviewed by E. O Wilson” (Schopf 1972a; Schopf, “Notes on 1956–1976,” 5 July 1976: Schopf pap. 7, 1). Additionally, while still completing the Models volume, Schopf wrote a paper, entitled “Ergonomics of Polymorphism: Its Relation to the Colony as the Unit of Natural Selection in Species of the Phylum Ectoprocta,” that paid explicit homage to Wilson’s work on the caste system in ants. In that paper, Schopf examined polymorphism in bryozoans, which he likened to the caste structure Wilson had observed in ant colonies and had described as a form of “kin selection” (Schopf 1973, 259). In the acknowledgements, Schopf thanked Wilson for conversations that
had led to the paper’s conception and for commenting “extensively” on the manuscript. Schopf noted in his autobiographical sketch that this paper foreshadowed a “general model of speciation” in Bryozoa, published in 1976, that presented “an equilibrium model using stochastic processes (Schopf 1976a).

Schopf’s most explicit early theoretical engagement with equilibrium models came in his introduction to the *Models* volume, “Varieties of Paleobiologic Experience.” In this essay Schopf examined a variety of theoretical approaches to paleontology, but focused especially on equilibrium models, which he likened to “gas law[s] in which the state of any particular molecule is immaterial to the general description of the behavior of the volume as a whole.” The value of such an approach, he argued, would be that “where the particular history of species may be immaterial . . . in some important senses, every species is ‘equally good’” (Schopf 1972b, 12–13). Schopf drew an analogy between this “particle paleontology” and the MacArthur-Wilson equilibrium model in that the evolutionary history of an individual species might be ignored, just as the life history of an individual island colonizer was merely part of the statistical dynamic steady-state of arrival and extinction. In either case, the behavior of individuals in the system is essentially stochastic, but the behavior of the whole is predictable. Ultimately, this perspective would lead Schopf to determine— as he explained in his 1976 personal narrative—that “the basis for any general theory of the history of life is, I feel, in investigating equilibrium models in which stochastic processes are the important processes” (Schopf, “Notes on 1959–1976”: Schopf pap. 7, 1). Schopf, therefore, can be regarded as one of the earliest and most significant conduits for the transfer of MacArthur-Wilson equilibrium biogeographical theory to paleobiology.

When Schopf set a date for the first Woods Hole meeting on the weekend of 26–27 August 1972, he wrote to Simberloff with details and a reading assignment (the newly published textbook *Principles of Paleontology*), and reminded him, “It is extremely critical that you be able to attend, since you have the mathematical expertise, and the first hand experience with developing simple mathematical models” (Schopf to Simberloff, 27 March 1972: Schopf pap. 5, 34). Schopf also sent a short agenda to the three other participants, outlining the questions he hoped might be addressed during the meeting. In particular, he suggested attacking the conventional emphasis in invertebrate paleontology “on the facts of history, often stressing unique events” that “has led to historical models where the ideas are closely tied to empirical summaries.” As examples of this approach Schopf cited Valentine’s 1969 paper on increasing marine diversity over time, A. Lee McAlester’s correlation of historical variations in oxygen with major periods of extinction, and Frank Stehli’s correlation of global diversity patterns with temperature fluctuations (Schopf to Raup, Gould, and Simberloff, 20 April 1972: Schopf pap. 3, 30). Schopf suggested that “one way we could proceed would be to examine these and other patterns in terms of equilibrium models,” an approach he noted which “worked extremely well in a field very similar to ours, i.e., biogeography, with the species equilibrium.” Schopf then presented the four initial problems to be explained—the investigation of “organismal diversity,” “morphological themes,” “chemical themes,” and “phylogeny” through time—and suggested, “We want to ask what are the processes underlying these patterns, and what are their long-term equilibrium consequences” (Schopf to Raup, Gould, and Simberloff, 20 April 1972: Schopf pap. 3, 30).

It seems that Schopf hoped to develop some kind of approach to analyzing fossil data using sources like the *Treatise on Invertebrate Paleontology* or the 1967 compilation *The Fossil Record* to produce generalizations similar to the MacArthur-Wilson island model. Raup recalls that “the original meeting in Woods Hole was stimulated by the success of island biogeography (MacArthur-Wilson),” and that “Tom hoped to apply the same thinking to the Phanerozoic record” (Raup, e-mail communication with John Huss, 13 March 2002). Raup also remembers that Schopf brought the entire multivolume *Treatise* to the meeting, “and we put it on the table” while Simberloff brought one of the earliest programmable hand calculators. “The question was: ‘What can we do that’s different?’” (Raup, quoted in Sepkoski 2009, 463). Unfortunately, Schopf’s hopes were dashed. Simberloff recalls that “right at the start they presented me with a whole raft of paleo data and patterns,” but that he immediately had “problems with analyzing all of them in ecological terms, largely centering on the fragmentary nature of the data” (Daniel S. Simberloff, e-mail communication with John Huss, 15 March 2002). In other words, the plan seemed to have optimistically hinged on Simberloff’s ability to work his mathematical magic on the data, and fallback options had apparently not been considered. Or, as Raup succinctly summarizes, “We got nowhere. Dead zero” (Raup, quoted in Sepkoski 2009, 463).

However, this initial failure had the effect of producing an unexpected
new direction. Frustrated by three days with little success, and in some desperation on the final afternoon of the meeting, Raup posed a radical idea. He effectively asked, “What if we take natural selection out of the equation?” More specifically, he proposed simulating the history of life as if it were random—“that is, if extinction or survival of lineages was merely chance”—to serve as a null hypothesis against which to test the traditional evolutionary assumption that phylogenetic patterns observed in the fossil record are solely the result of deterministic and directional processes. As Raup explained, “The idea was not meant to suggest that things like the extinction of species occur without cause. Rather, that there are so many different causes of extinction operating in any complex ecosystem that ensembles of extinctions may behave as if governed by chance alone” (Raup, quoted in Sepkoski 2009, 463). Since the meeting was over, Raup volunteered to write a computer simulation program and report back to the group.

This, in essence, was the genesis of the MBL model. However, before moving on to consideration of the MBL papers themselves, there are two additional influences that need to be addressed. The first concerns the source of the introduction of stochastic or random models. Despite Schopf’s later contention that he was led directly to consider random processes by his interest in equilibrium models, there is no evidence in his work prior to the MBL meetings that he had given stochastic models any thought. Gould also would have been an unlikely source for this idea, given that he has explicitly described his theory of punctuated equilibria (at least in its original inception) as a deterministic, even “Darwinian” model. This leaves Raup, who, in 1969, published a paper (with Adolph Seilacher) on a “grazing track model” for analyzing trace fossils that described the grazing patterns of individual animals as “partially stochastic” (Raup and Seilacher 1969). Although the paper did not involve detailed analysis of stochastic factors, it did indicate that Raup had previously developed some familiarity with mathematical treatments of randomness. Since Raup confirms that by 1972 he was “far enough along with random number generators” that writing the original MBL program posed no great difficulty, it is entirely possible that this was the inspiration for generating random phylogenetic trees (Raup, quoted in Sepkoski 2009, 464).

There is other evidence that Raup came to the meeting prepared to discuss random models. In a letter to Schopf prior to the first MBL meeting, Simberloff made the suggestion that “another model type” (i.e., another theorist) be invited to the meeting, “someone especially at home with stochastic models (which may be what turns out to be appropriate for paleontology)” (Simberloff to Schopf, 19 April 1972: Schopf pap. 5, 34). Schopf mentioned in the agenda sent to all participants that “Dan felt that we should consider the role of stochastic models, and in particular that someone with this background be involved.” However, Schopf also concluded “that unless the issues are fairly clearly delineated, that just the four of us should meet this first time” (Schopf to Raup, Gould, and Simberloff, 20 April 1972: Schopf pap. 3, 30). In response to this letter, Raup replied “I am a strong advocate of stochastic models, as you know,” but also cautioned “they are, as you know, dangerous as hell,” and he endorsed Schopf’s cautious stance that “stochastic models will come up where appropriate—but that they should not be treated as ends in themselves” (Raup to Schopf, 27 April 1972: Schopf pap. 3, 30).

The second influence was University of Chicago evolutionary theorist Leigh Van Valen’s so-called Red Queen’s Hypothesis. Although the idea was first proposed in a paper (entitled “A New Evolutionary Law”) published a year after the initial MBL meeting, as Van Valen noted, his ideas had “been circulating in samizdat since December, 1972,” and he thanked both Schopf and Raup in the acknowledgements of the paper for previous discussions (Van Valen 1973, 21–2). It is clear, then, that members of the MBL group were aware of Van Valen’s paper while they were developing their own initial model, and Raup has stressed that any discussion of “important historical elements [in the MBL story] must include Van Valen’s original [1973] Red Queen paper” (Raup, e-mail correspondence with John Huss, 13 March 2002).

The Red Queen’s Hypothesis would have an important influence not just on the MBL models, but also on the debates over taxonomic diversity that will be discussed in the next chapter. Van Valen’s argument was essentially a reexamination of the application of survivorship curves used in population ecology to paleontology. From the time of Simpson’s Tempo and Mode, survivorship curves—expressed as a plot showing the probability of an individual’s extinction with age—were a standard method in paleontology for depicting the longevity of taxa. While Simpson and other paleontologists had plotted survivorship arithmetically, one of Van Valen’s innovations was to plot his own survivorship curves with a logarithmic ordinate—as was standard in population ecology—which meant “that the slope of the curve at any age is proportional to the probability of extinction at that age” (Van Valen 1973, 1). Van Valen
also plotted survivorship curves for much larger samples than Simpson had used: his initial study analyzed the first and last appearances in the fossil record of more than 25,000 subtaxa of vertebrates, invertebrates, and plants. Conventional wisdom was that a taxon’s probability of extinction increased with its longevity. However, Van Valen’s results confounded this expectation: his survivorship curves were linear (plotted on a logarithmic ordinate), which meant that the probability of extinction for a subtaxon within a given group remained constant over time. In other words, according to Van Valen’s analysis, there is no correlation between the age of a taxon and its probability of extinction; within a higher taxonomic group, extinction rates are effectively constant, and all subtaxa have an equal probability of extinction at any given time—regardless of age.

Van Valen’s paper explored the meaning of this result, which he interpreted in an ecological context as an evolutionary ‘law’: “The effective environment of the members of any homogeneous group of organisms deteriorates at a stochastically constant rate,” or “extinction in any adaptive zone occurs at a stochastically constant rate” (Van Valen 1973, 16). Van Valen explained this result with a metaphor drawn from Lewis Carroll’s *Through the Looking Glass*, where the character of the Red Queen proclaimed, “Now, here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!” In the face of ecological pressures, Van Valen argued, “each species is part of a zero-sum game against other species,” in which “no species can ever win, and new adversaries grinningly replace the losers” (Van Valen 1973, 21). Because of this, each species must keep “running” just to maintain its fitness from one moment to the next. Since the age of a given taxon neither detracts nor adds to its momentary fitness, “the probability of extinction of a taxon is then effectively independent of its age” (Van Valen 1973, 17). Van Valen’s hypothesis was potentially revolutionary because it was unsettling to conventional assumptions about evolution, as Van Valen himself acknowledged at the end of his paper:

> From this overlook we see dynamic equilibria on an immense scale, determining much of the course of evolution by their self-perpetuating fluctuations. This is a novel way of looking at the world, one with which I am not yet comfortable. But I have not yet found evidence against it, and it does make visible new paths and it may even approach reality (Van Valen 1973, 21).

The major influence this idea had on the MBL model was that it justified the assumption that the evolutionary properties of species (or other subtaxa) are essentially “equivalent,” which in turn endorsed the construction of a model in which species could be treated as identical “particles” in space and time (Huss 2004, 58–60). This was part of the “novel way of looking at the world” Van Valen referred to, and as we will see, the MBL model would eventually test the comfort each of the participants felt in employing it.

The Initial MBL Model

In the fall of 1973, Schopf addressed a letter to Raup, Gould, and Simberloff that began “Dear Fellows of the ‘Radical Fringe of Paleontology’” (Schopf to Raup, Gould, and Simberloff, undated [fall 1973]: Schopf pap. 3, 30). This was just one of several nicknames that the group would acquire; they would be variously labeled elsewhere as the “gang of four” and “the four horsemen of the MBL.” There was indeed something quite radical about the MBL model, and in many ways the very first paper, “Stochastic Models of Phylogeny and the Evolution of Diversity,” which appeared in late 1973, was the most radical of the entire sequence.

One of the ironies of this story is that such a bold, theoretical paper—a paper that declared itself to be “the first in a projected series of papers that might bear the general title ‘nomothetic paleontology’”—was published in the very conservative *Journal of Geology*, which had a traditional emphasis on hard-rock geology and a fairly limited circulation (Raup et al. 1973, 526). However, it turns out the choice of venue had less to do with exposure than with expediency: the *Journal of Geology* was owned by the University of Chicago, and Schopf, whose office was in the “same building” as the journal’s, was able to arrange for quick, uncomplicated approval and publication (Raup interview). This is an important reminder that conceptual developments cannot be separated from institutional resources and context: in the days before *Paleobiology*, paleontologists faced limited options and sometimes daunting obstacles to getting theoretical papers published. In fact, Van Valen became so frustrated with the policies of established journals that he founded his own journal, *Evolutionary Theory* (where the original Red Queen paper and

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1. The “four horsemen” reference was Phil Signor’s, and was not a compliment (Signor to Jack Sepkoski, 7 June 1981. Sepkoski pap. ‘1981’).
many of his subsequent papers appeared), which for many years he pro-
duced on a mimeograph machine in his own office.

From its opening lines, the first MBL paper announced its debt to the
MacArthur-Wilson equilibrium model, and also the hopes that its au-
thors had to imitate the success of that research program:

The application of equilibrium models to population biology and theoretical
ecology has yielded important generalizations and redirected field explo-
ation. Most striking has been the direction of animal biogeography away from a
purely descriptive summation of distributions toward the prediction that
species diversity is in equilibrium dependent upon immigration rates, extinc-
tion rates, and the area available for colonization. . . . This result raises major
questions about the guiding principles behind evolution—in particular, can the
processes resulting in local equilibria in ecologic time also be used to pre-
dict events in evolutionary time? (Raup et al. 1973, 525)

The paper began with the basic observation that equilibrial diversity
models, developed to describe populations of organisms in ecological time,
might have a fruitful translation to the fossil record and geologic time.
This observation would be at the heart of both the MBL model
and the subsequent debates over Phanerozoic diversity. Here it was ex-
pressed as “a continuation of the conscious application of equilibrium
models to paleontological data,” and an attempt to determine “whether an
equilibrium pattern of phyletic radiation can exist, and if so, what its
characteristics would be” (Raup et al. 1973, 525).

This initial paper also promoted a new, idealized approach to read-
ing the fossil record. As the authors noted, “The essential assumption of
this strategy is that the true complexity of events in the real world can be
adequately rendered by models using relatively few generating factors.”
They pointed to the success of this program in theoretical ecology, a dis-
cipline they characterized as “nomothetic,” in contrast to paleontology,
which “has traditionally focused on the idiographic (Why did this crinoid
become extinct at that time).” For their own part, Raup et al. expressed
determination to “try to abstract the common elements hidden be-
nenath the bewildering and all but impenetrable verbiage of our nomen-
clature and stratigraphy by constructing a model that makes no reference
to individual taxa” (Raup et al. 1973, 526). One of the unstated advan-
tages of this nomothetic approach to paleontology was that it rather con-
veniently freed its adherents from their dependency on the notoriously
fragmentary and unreliable fossil record. However, this point was not
belabored in the first paper, nor was it mentioned that the paper’s central
idea originated in response to the explicit failure of the group to make
headway with actual fossil data.

The basic MBL model itself was quite simple: Raup had designed a
computer program that simulated the evolution of phylogenies by gen-
erating an initial “lineage” and then randomly subjecting it and its “off-
spring” to one of three possible outcomes—extinction, persistence with
branching, or persistence unchanged—over a predetermined number of
steps. This was an application of a randomization process known as a
Monte Carlo simulation. The computer was used to randomly draw
numbers to determine outcomes with prespecified possibilities, much as
a dealer might randomly draw cards from a deck and arrange the out-
comes into hands. At the end of the run, the program output the results
graphically in the form of a branching phylogenetic tree. The program
also automatically grouped lineages into “clades” when lineages had ac-
cumulated a preset number of branches. These clades were graphically
depicted in “spindle diagrams” representing clade diversity, in which the
width of the spindle varied in proportion to the number of lineages it
represented (fig. 7.1). Both kinds of graphical representations would have
been “instantly recognizable” to paleontologists (Huss 2004, 63–64).

In addition to these basic parameters, a few additional controls were
built into the program. Most significant was the adjustment of the prob-
abilities set for extinction and branching at each step, in which the initial
probability of extinction was damped so that branching was favored. As
the program approached a predetermined “equilibrium diversity,” the
probabilities of extinction and branching were equalized so that divers-
ity would oscillate around a mean equilibrium value. Raup does not re-
member this constraint having been motivated by any explicit biological
assumptions, but rather that it addressed the limitations of early 1970s
computer technology. Because of limited computer memory, if the ini-
tial probability of extinction were too high, most runs would simply ter-
minate after only a few steps. On the other hand, if no equilibrium value
were set, the program would quickly generate too many lineages for the
computer to handle (only 500 lineages could be stored in the computer’s
memory at any time). In the final paper, the authors recast this technical
limitation as an explicit endorsement of the MacArthur-Wilson model,
explaining, “We did not choose to limit diversity simply to restrict a
potentially boundless phylogeny to a tractable size.” Rather, “the maintenance of an equilibrium diversity in the present work implies that an adaptive zone or a geographic area becomes saturated with taxa and remains in a dynamic equilibrium determined by the opposing forces of branching (speciation) and extinction.” This they directly attributed to the influence of the MacArthur-Wilson model (Raup et al. 1973, 529).

“I grant that the equilibrium aspect came to be important but I certainly did not think this way while formulating the MBL program,” Raup recalls. “I used an equilibrium constraint in the MBL algorithm only as a protection against saturating the computer’s memory. Given my wish to make MBL constraint-free, I would not have included a control on population unless forced to.” Nonetheless, reflecting on this fact nearly 40 years later, Raup concedes, “I [recently] opened the original paper and was astonished to see Equilibrium as the first word of the abstract and to read the emphasis on equilibrium throughout the paper. . . . Was our thinking recast as the project developed, or is my memory playing tricks?” The most likely explanation is that Raup’s solution to a technical problem was seized on by the more equilibrial-minded collaborators (Schopf and Simberloff) as a serendipitous endorsement of their own theoretical predilections. “I submit that most of our interesting results could have been achieved with [an] unconstrained algorithm,” says Raup. “I suppose my colleagues would have eventually insisted on adding equilibrium” (Raup, personal communication, 29 April 2010).

The MacArthur-Wilson model was only one of three major assumptions about the dynamics of evolution that the MBL program accommodated. The second had to do with the way evolution was reflected in the model. Since lineages could change only by branching and persistence of the original lineage, the phenomenon of “pseudo-extinction,” in which lineages gradually transformed from one to another, was excluded from the model. This was an explicit accommodation of punctuated equilibria; as the authors explained, the MBL model “describes a situation in which phyletic transformation is absent and where new taxa arise only through speciation,” pointing out that “Eldredge and Gould (1972) have argued that it corresponds closely to biological reality” (Raup et al. 1973, 528). The third assumption related to extinction. As Huss observes, Van Valen’s Red Queen’s Hypothesis provided two important justifications for the MBL model. First, it validated treating individual taxa as essentially identical units, since Van Valen had shown that despite individual differences average rates of extinction should be the same for all taxa.
Second, the Red Queen justified the assumption of stochastically constant rates of extinction, and endorsed choosing a resolution level that ignored individual selection. However, Huss also notes, “In applying Van Valen’s ideas, MBL excised his causal language and his distinctions between causal mechanisms and their resultant patterns,” while retaining the “mathematical behavior” of the phenomenon being described. Huss sees this as “inevitable” and “perhaps the whole point of a mathematical model” (Huss 2004).

There are other significant features of the MBL model worth discussing. First, it helped to introduce stochastic null hypotheses into paleobiological modeling. The model was not assumed to depict any actual mechanisms or processes in the real world; rather, in excluding traditional deterministic evolutionary assumptions, it implicitly tested those very assumptions. As the authors explained, “We do not suggest that evolution be viewed as a haphazard process, independent of basic relations of cause and effect.” Nonetheless, “We wished to predict what phylogeny would look like if it were determined by random processes and then to compare this with the real world, to enable us to separate random elements from those that require interpretation in terms of specific and perhaps nonrecurring causes” (Raup et al. 1973, 526–27). In other words, the null hypothesis of randomness should be examined and dismissed before assumptions of determinism are accepted. If the null model could not be easily dismissed, than traditional assumptions would have to be re-examined.

Second, the results of the initial study confirmed the importance of statistical random walks in the interpretation of patterns of evolution and extinction. The authors tested their simulations against actual diversity data in 178 higher taxa of reptiles drawn from The Fossil Record (Harland 1967). In doing so, they found a number of striking similarities between the real and simulated clades. To take one example, the characteristic shape of the simulated spindles—a tendency to taper on both ends and bulge in the middle—was similar to about two-thirds of the reptile clades (Raup et al. 1973, 538). For another, the pattern of initial rapid diversification with low extinction values, tapering off at an equilibrium level where speciation and extinction were roughly equal, was clearly evident in both real and simulated clades (Raup et al. 1973, 539). How could this similarity be explained? Another way of putting it is to ask how an apparently random process produced patterns of apparent directionality and biological “meaning.” The initial 1973 paper did not explore these apparent similarities in detail, but follow-up publications (as we will see) applied the concept of the random walk as an explanation for how random factors can produce apparently directional patterns. This conception invoked a special kind of statistical process known as a Markov chain, which became an important explanatory tool in analytic paleobiology.

Finally, the simulations performed in the initial paper represented a new and important current in the application of computer technology to paleontological data, where computers were used not just as calculating tools, but as sites for the construction and testing of novel hypotheses. This is similar to Raup’s simulation and analysis of coiled shell morphology. In both cases, the computer performed two very important functions in addition to crunching numbers: First, computers allowed for a kind of idealized “experimentation” that would not have otherwise been possible in a historical discipline like paleontology. In the late 1960s, Raup was able to manipulate and produce hypothetical shell morphologies that are not necessarily found in nature, which in turn allowed him to reach conclusions about the constraints that govern the structure of actual organisms. Similarly, the MBL model allowed paleontologists to experiment with patterns in the fossil record—it gave paleontologists the ability to “rewind the tape of life,” in Gould’s later memorable phrase, and to produce counterfactual or alternative histories that allowed paleontologists to interrogate the actual record in new and interesting ways. Huss discusses the importance of this kind of “numerical experimentation,” which he defines as “the practice of creating mathematically modeled reality within which experiment is conducted via simulation” (Huss 2004, 150). Second, computers introduced an important and new kind of visual imagery into paleobiology. Raup’s computer-generated shells are one obvious example of this; the graphical output of the MBL program is another. In both cases, the visual imagery itself was as important in the arguments being put forward as was the text presenting the data, and are examples of what Jan Golinski calls a “visual hermeneutics” (Golinski 2005, ch. 4). It was the striking visual representation of simulated clades that was often most compelling to paleontologists who read these papers; as Huss puts it, “The most salient argument remained a visual argument based on an overall gestalt, the likes of which had been doing the heavy lifting” since the first MBL paper (Huss 2009, 336).

The 1973 paper certainly raised more questions than it attempted to provide answers for. The authors quite readily acknowledged that their
analysis “has been primitive so far,” and pointed out a number of potential problems with analogies they had made between real and simulated data (Raup et al. 1973, 539). What they did propose was that the simulation experiments potentially challenged many traditional assumptions in interpreting—or “reading”—the pattern of the fossil record:

When faced with such variation in evolutionary patterns, paleontologists are inclined to suspect or even to postulate that the organisms involved are inherently different—that the various taxonomic groups differ from one another because they differ in population structure, reproductive systems, mutation rates, dispersal systems, and so on.

In other words, paleontologists traditionally assumed that the fossil record looks the way it does because individual and specific ecological and biological constraints have determined that the history of life must look this way, and no other.

But the simulation modeling shows that two or more groups operating under identical constraints—that is, having the same evolutionary potential—can behave very differently. We do not rule out that such differences in the real world may be due to inherent biological differences. We only contend that the observed variation does not in itself demand such an explanation (Raup et al. 1973, 534).

The salient point here was not that traditional paleontological explanations were necessarily wrong, only that they might be underdetermined by available evidence. Raup et al. warned “above all . . . against using patterns of diversity as the major evidence for differences in evolutionary potential.” The question that would be pursued in succeeding MBL papers—and which would surface behind the scenes in the next several years this tension would grow, and Gould would find himself in the role of mediator between the two.

Schopf had originally hoped to have the MBL group convene during the 1973 GSA meeting in Dallas, but schedule conflicts made a Christmastime gathering back in Woods Hole more feasible. In September of that year Schopf wrote to Gould to thank him for “your gracious remarks to Dave [Raup] about my overblown writing on the importance of our meetings, and what has come of it” (Schopf to Gould, 27 January 1973: Schopf pap. 5, 14). It is unclear to what Schopf was referring, or if he even sent the letter (the version that appears on Schopf’s departmental letterhead has a handwritten note reading “not sent”), but this is an early indication that Schopf, who would continue to press for a more “radical” interpretation of the MBL model, was already butting horns with Raup, who would favor a more conservative one. Over the next several years this tension would grow, and Gould would find himself in the role of mediator between the two.

Schopf’s letter began by characterizing his initial motivation for bringing the group together as “the romantic, idealistic notion that Paleontology, rich in evidence, weak in theory, nearly devoid of equilibrium models . . . could be redirected by the self-conscious application of a way of doing science not found previously in paleontology.” He explained that while he maintained his hope that “our relative strengths could be dedicated to a higher purpose which would result in a quantum increase in understanding the biological meaning of the fossil record,” it was becoming clear that “there is some difference of opin-
“Towards a Nomothetic Paleontology”

While we were close enough together on the first paper that this was not a serious problem, the situation has obviously fallen apart with the [Raup and Gould] morphology paper, and the odd situation of my ending up writing a geological paper which called for a short explicit test that Dan was then able to provide. Accordingly we really have gone our separate ways, and without a face-to-face meeting of the 4 of us again to reestablish possibilities for mutual input, I think we will continue to go our various ways (Schopf to Gould, Raup, and Simberloff, 28 September 1973: Schopf pap. 5, 30).

Even so, Schopf was not ultimately pessimistic. “I think that our base intellectual input is so unique and powerful that it will have the desired effect,” he wrote. “I cannot help but think that this approach will revolutionize the fundamental questions that are asked in paleontology.” He closed the letter by suggesting that the group consider sponsoring a “joint course or workshop stressing stochastic processes, and equilibrium theory, in the context of the fossil record in particular, and evolutionary biology in general,” which could be aimed at a broad audience of paleontologists and offered at some point in the next year or two.

In his response, Gould (perhaps surprisingly) conceded many of Schopf’s points, though he remained unequivocally convinced of the importance of the research program. He went on to reassure Schopf:

You are right in arguing that we are among the first group of scientists to use a consciously nomothetic approach to paleontology (there’s that word again, but it’s the right one and I don’t apologize). Previous explanatory schemes have been either particularistic (functional morphology of this or that group), general theoretic applied to particulars (biogenetic law) or representative of that curious technique of theorizing that tries to establish general laws by induction from historical facts (Cope’s law etc.). . . . The more you think about it, the more you realize how heretical the search for a kind of timeless generality appears within a science so deeply committed to historicity. . . . The only reason we may not cause the stir we should is that paleontologists are so notoriously unaware of the philosophical implications of their methodologies (Gould to Schopf, 5 October 1973: Schopf pap. 5, 14).

He therefore encouraged continued meetings “if we are to reestablish mutual input—and I think we owe such a meeting to what we have already done,” and endorsed the idea of a public workshop to spread the new ideas. This was apparently enough to keep the collaboration going; the next letter from Schopf is the one which bears the cheeky heading “Radical Fringe in Paleontology,” and it set out the arrangements for the next meeting.

Simulated Morphologies, Directional Evolution, and Markov Chains

Gould’s reassurances aside, Schopf’s concern had not been unfounded. Raup and Gould’s morphology paper—“Stochastic Simulation and Evolution of Morphology: Towards a Nomothetic Paleontology”—was perhaps the most important and original of the entire sequence. It would not be surprising if Schopf felt left out, and even hurt, at being excluded. Whereas the original MBL paper simulated evolution and extinction in lineages that had no individual characteristics, Raup and Gould modified the MBL program to simulate a randomly changing “morphology” consisting of a set of hypothetical “characters” that randomly “evolved” at each step in the program. Whereas the first study had asked, “What would diversity look like in the absence of selection?,” Raup and Gould now asked, “What would trends in morphology look like without unidirectional selection?” The importance of this modification was that it allowed a more sophisticated interrogation of the assumption that directional trends were the product of “directed causes”: as the authors explained,

Modern paleontology has retained a vestige of idealistic morphology in its traditional argument for the role of directional causes in macroevolution. The presence of order in the results of evolution is taken uncritically as definite evidence for the production of such order by directed causes. . . . The marks of order include evolutionary trends, correlation between characters, and morphological coherence of taxonomic groups. The postulated cause, for the last thirty years at least, has been uni-directional selection (Raup and Gould 1974, 305).
This question was a logical extension of the discussion Eldredge had appended to the first draft of the 1972 punctuated equilibria paper, which had essentially asked, “How do we explain trends?” Raup and Gould responded in this paper that “we have come to doubt that the formal pattern of change is an adequate argument for directed causes,” and suggested that apparent order “can arise in random systems of change, bounded only by the conventional assumptions of monophyly, continuity, and equilibrium” (Raup and Gould 1974, 306). The surprising result they announced was that directional selection was not needed to produce apparent trends in morphology.

Raup and Gould defended the biological assumptions in their model by arguing that random morphological changes could be imagined to have been produced either as adaptive responses to random fluctuations in environment, or by genome alteration produced by random drift. Thus, the model was neutral towards “Darwinian” or “non-Darwinian” evolutionary interpretations. The null hypothesis it set out to test was the assumption that directional selection was required to produce evolutionary order: if apparent order could be produced without directional causes, then paleontologists would be justified in looking beyond orthoselection for other mechanisms that could produce directional trends (Raup and Gould 1974, 306). In many ways this question was a natural outgrowth of previously established commitments of both authors. Gould had primarily explored the role of mathematical allometric relationships as constraints on morphologic evolution, while Raup had similarly investigated geometric constraints in his simulations of theoretical morphospace (Gould 1966).

Raup and Gould made a number of runs of their simulation, which assigned a set of hypothetical “characters” to an original ancestral “lineage,” and tracked the changes in those characters over successive branching points. They then examined the results by comparing them to expectations for what they termed the “general orderliness” in an evolutionary tree. In the first place, they argued, in a nonrandom evolutionary tree we would expect to see an incomplete filling of morphospace; the traditional assumption is that morphological similarities along an ancestral line are a function of recency of ancestry, which constrains the degree of departure from the initial state. This incomplete filling might also be taken as evidence of selection, wherein morphospace would be “colonized” in a nonrandom way as selection pursued certain advanta-
evolutionary order did not exist. However, Raup and Gould argued that the simulation cast doubt on certain traditional assumptions in paleontology. First, they stressed that the assumption that apparent directional changes in morphology are necessarily produced by deterministic causes—whether “internal factors in the bad old days of orthogenesis and vitalism” or “directional selection today”—was misplaced. As the simulation showed, trends “of outstanding duration and unreversed direction” could be produced by random factors alone (Raup and Gould 1974, 314). Second, while an inductive approach to functional morphology assumes some causal basis for correlations among characteristics (e.g., shell volume and number of whorls in a chambered nautilus), strong correlations between characters were produced in the simulation in the absence of any causal relationship between characters. For the 200 lineages simulated, correlation coefficients for the 45 possible pairs of character states showed that 75% of pairs yielded statistically significant correlations. As Raup and Gould put it, if this “were encountered in the real world, we could usually assume either that the characters are not genetically independent, or that there is a functional or structural relationship between them, such that the expression of one is effectively dependent on the other.” Of course, in the simulation no such relationship existed (Raup and Gould 1974, 314–15). Third, significant variation in rates of morphological change is usually interpreted as evidence of “real biological differences among structures subjected to unidirectional selection.” Put simply, different kinds of organisms (e.g., clams versus mammals) should evolve at different rates because of inherent biological/genetic differences. In the simulation, all characters should have evolved—on average—at the same rate, because there were no inherent differences between ‘organisms.’ However, the simulation produced different rates of morphological evolution in different lineages, suggesting that “the operation of chance” is enough to account for differences between rates of evolution among different taxa (Raup and Gould 1974, 316). Fourth, Raup and Gould argued that the simulation made a positive case for the significance of episodes of evolutionary convergence, which the authors noted are “widely regarded as crucial tests for the understanding of natural selection,” since they act as ‘natural experiments’ for testing hypotheses about the efficiency with which natural selection responds to adaptive problems. In the simulation, convergence was represented by similar character states in widely separated lineages, and we would expect phenetic reclassifica-

tion to group convergent lineages more closely than their phylogenetic relationships warrant. However, this did not happen: convergence was not a phenomenon in the simulations. Raup and Gould explained that this suggested convergence may be a genuine result of “unidirectional selection for (presumably) functional adaptation” (Raup and Gould 1974, 316–17). Finally, the simulation shed light on the consequences of evolutionary specialization. It had often been assumed that “terminal overspecialization”—that is, the tendency of some lineages to develop such overspecialized characteristics that no longer had adaptive value (e.g., the antlers of the Irish elk)—was the result of some intrinsic law that defined ideal adaptive parameters (e.g., Cope’s Law). However, in the simulation extreme morphological values (high positive or negative numbers for individual characters) were found at the terminal end of lineages simply because they had had greater opportunity to diverge. Overspecialization in nature, then, might just be a product of chance over time (Raup and Gould 1974, 317–18).

Raup and Gould summarized their results with a striking visual example: in order to make the simulation results more concrete, they arbitrarily assigned each of five of the simulated characters a morphological ‘value’ to create an imaginary organism they named a “triloboid.” These triloboids were then represented along 11 of the simulated clades, so that the evolution of their morphology could be graphically depicted (fig. 7.2). The graphical representation alone made a strong visual argument: the evolution of each triloboid lineage looked realistic in the sense that while “they display considerable morphological variation,” they nonetheless shared characteristics that appear common to the clade as a whole. As the authors put it, if this imaginary example “depicted an actual case, it would probably not stand out as unusual: the relation between cladistics and phenetics presents a plausible picture” (Raup and Gould 1974, 319). The results of this simulation, then, seemed to lend support to the argument that many paleontological assumptions about trends were underdetermined by evidence. If apparently directional trends could be produced by random generation, then many of those assumptions would need to be reexamined.

However, this did not explain why these random simulations had the ability to mimic directional patterns. Here Raup and Gould leaned heavily on the statistical concept of the random walk, a particular kind of result produced by a special statistical process known as a Markov chain, in which the probability of a future event is independent of the
configuration of past events. Markovian processes are notable because they often produce apparently directional patterns even though the overall system is stochastic. Take, for example, a series of coin flips. This is a Markovian process, since the result of successive flips are in no way conditioned by prior throws. Whether or not the next flip will be heads or tails has nothing to do with previous results. A Markov chain reflects no “memory” of past events, and future outcomes are dependent only on the states that immediately preceded them. Imagine a series of coins are flipped, but that after each toss the result is plotted on a graph, with each flip moving one step forward on the abscissa (x-axis), each “heads” indicating a positive step on the ordinate (y-axis), and “tails” a negative one. Each flip has equal probability of being heads or tails, but the pattern of flips will likely show strong directionality, because each successive step can only be one unit above or below the previous one. Furthermore, the probability of heads or tails is reset after each flip; the coin does not “know” that after several successive heads it is due for a tails. Thus, as the number of flips increases and the graph moves forward along the abscissa, there is a strong likelihood that directional patterns will be produced—for example, that the points will “walk” on the positive side of the ordinate for some or all of the run. Markov processes therefore have the ability to generate directional patterns from otherwise random events; in fact, when tested with conventional statistics most random walks produce statistically significant trends (so-called nonsense correlations).

The morphological version of the MBL model presented by Raup and Gould is a Markov process. As Huss puts it, “A lineage’s morphology in large part reflects the morphology of its ancestor, since each character of a given lineage in a given interval will vary at most by one increment or decrement of one unit from the state of its most immediate ancestor” (Huss 2004, 78). The randomization function of the program was counterbalanced by the provision that each successive state is based only on the immediately preceding one, therefore constraining possible changes from one time-unit to the next. For example, a character state could not jump from “1,3,-2,1,2” to “5,5,5,5,5” in a single step; in practice, lineages tended to be quickly constrained in a particular direction, and change occurred very slowly and gradually.

Raup and Gould recognized this feature of their simulation, from which they extrapolated a broader conclusion: that “the basic order of morphology on an evolutionary tree need not reflect any special biological process, but arises inevitably . . . from topological properties of the abstract form of the tree itself” (Raup and Gould 1974, 320). In other words, that there are certain predictions that can be made about the properties of an evolutionary tree based solely on the laws of probability, irrespective of any particular biological processes. One example is what they termed the “spreading effect,” which predicts that lineages which by chance quickly produce a large number of descendents will establish a “crowded” region of morphospace filled with “near replicates.” Since morphologic change is gradual, this region will be the center from which subsequent morphological variations will slowly ‘spread,’ leaving large regions of morphospace unoccupied. This will tend to happen whether or not particular morphologies are assigned adaptive ‘values.’ Another example relates to the “irreversibility” of morphological evolution: if we consider the initial ancestral character state to be “un-specialized” (i.e., set to values of zero), it is inevitable that successive branchings will produce ever more “specialized” states as the simulation walks from one step to the next. With each step, due to the number of characters involved, it becomes increasingly unlikely that a previ-
ous state can ever be recovered. Again, this takes place without respect to any selective value in the character states. In both of these examples, a result which had been normally attributed to deterministic biological factors could be demonstrated to follow logically from the basic rules of probability (Raup and Gould 1974, 321).

Despite this potentially profound challenge to the logic of traditional paleontological (and Darwinian) approaches to selection and evolution, Raup and Gould insisted that their paper was “not an attack upon the concept of uni-directional selection.” Nonetheless, they did offer two conclusions: their “methodological” conclusion related to biologists’ tendency to infer evolutionary insight from the “abstract geometry of form,” a tradition stretching well back before Darwin. Since the simulation showed that “random processes can produce most of the patterns generally associated with directional causes,” it “constitutes a challenge to the formalist position.” Raup and Gould hoped that as a cautionary lesson, their paper would encourage “more attention” to the study of functional morphology, and to the principle that “adaptation is better demonstrated by the mechanics of form in relation to environment than by evidences of directional change through time.” The second, “substantive” conclusion was somewhat more iconoclastic: “The fact that examples of steadily changing characters do not occur with much higher frequency in the fossil record than in the computer simulations suggests that, over long stretches of time, undirected selection may be the rule rather than the exception in nature” (Raup and Gould 1974, 321).

More broadly, the results of the paper appeared to invite to two possible interpretations of the role of randomness in the history of life: a conservative interpretation was that the stochastic model was simply a useful heuristic for rethinking certain traditional assumptions in paleontology, but that it shed no light on the actual processes that govern evolution. A more radical interpretation drew the conclusion that evolution really is, in some ontological sense, a stochastic process. It seems that at the time of the paper’s publication, Raup and Gould were not in complete agreement. A short aside stated that whereas “one of us (SJG) remains an unrepentant Darwinian, the other (DMR) has his doubts” (Raup and Gould 1974, 321). However, the second, “substantive” conclusion suggests that both authors were seriously entertaining the radical interpretation of stochastic paleontology. The next phase in the development of the MBL model would bring this potential opposition into clearer focus, but it would also highlight divergent interpretations within the group, as each member considered, and reconsidered, the implications of a “stochastic view” of life.

**Implications of Stochastic Paleontology**

Although the entire MBL group would produce two more jointly authored papers, Raup and Gould’s morphology paper might be considered the high point of the collaboration (Schopf et al. 1975; Gould et al. 1977). Raup himself recalls, “Looking back over the MBL history, I think the (only?) really good paper is that with Steve Gould in 1974. And that was a wonderful experience: I did the analysis but Steve saw what it meant” (Raup, e-mail communication with John Huss, 14 March 2002).

While publications and other activities would continue through 1978, the group’s final meeting at Woods Hole was in December, 1973, shortly after the Raup-Gould paper was submitted to *Systematic Zoology*. After this point the MBL group would never regain its initial intensity and momentum, and internal tensions within the group would become more pronounced.

The final MBL meeting took place the weekend of 21–23 December, and discussion centered around how the original MBL program could be modified to address additional questions about rates and patterns of evolution. Gould’s graduate student Jack Sepkoski had been experimenting with different parameters and permutations of the program, and he was invited for the first two days to give a report of his findings. As Schopf put it in his letter to the group, “Modification of the program of course presupposes a purpose, and that will then lead to questions of what additionally we want the program to do for us,” and suggested that this might be “the time to bring out additional topics such as rates of evolution.” He closed the letter by reminding the group of his ambition to produce a book which would serve as a manual or primer on stochastic methods, for which Raup had agreed to write an initial outline (Schopf to Raup, Gould, and Simberloff, undated [circa November 1973]: Schopf pap. 3, 30).

The meeting appears to have been a success. By February of 1974 Sepkoski reported to Schopf that he had developed “a package of about 20 subroutines” based on Raup’s original code that included routines for analyzing numerical and cladistic taxonomy, survivorship curves,
and geological sampling. He noted that the new version of the program would be “more robust so that alternative hypotheses can be tested,” and promised a working version within the next several months (Sepkoski to Schopf, 21 February 1974: Schopf pp. 4, 60). In April, Sepkoski followed up with Schopf to report that the completed revision of the program was in Raup’s hands (Sepkoski to Schopf, 7 April 1974 (draft): Sepkoski pp. “1974”). Sepkoski’s involvement in the project was becoming increasingly important, although up to this point his role had been only as a technician. Gould had already employed him to write the program that performed the comparison between the phenetic and cladistic phylogenies for the morphology paper with Raup, and had mentioned to his colleague Richard Wassersug that Sepkoski was “the person most knowledgable about the computer program used in the Raup-Gould study” (Wassersug to Sepkoski, 10 April 1975: Sepkoski pp. “1975”). In addition to writing the MBL subroutines for Schopf, Sepkoski also provided him with a program he had written (QUAJAC, for Quantified Jaccard’s Coefficient) for performing cluster analysis on the MBL results. At the same time, Sepkoski was busy working on an improved database of first and last appearances of orders, families, and genera in the fossil record that Gould had commissioned to use for tests against the output of the simulated clades of the MBL program (Sepkoski 1994, 135).

7.3.1 Differential Evolutionary Rates

The result of the 1973 MBL meeting was the second “quadripartite-authored” MBL paper, “Genomic Versus Morphologic Rates of Evolution: Influence on Morphologic Complexity” (Schopf et al. 1975). This paper appeared in early 1975, in the very first issue of the new journal Paleobiology, alongside Raup’s important review of Van Valen’s Red Queen hypothesis (which will be discussed in the next chapter). The paper itself built on the analysis of morphological trends in Raup and Gould (1974) by directly addressing whether different groups of organisms have inherently different evolutionary clocks, or whether rather inherent rates of evolutionary change are effectively constant for all groups. Simpson had famously concluded in Major Features of Evolution that mammals, for example, had evolved more rapidly than bivalves by up to an order of magnitude, and this assumption was often taken for granted in paleontological literature. Schopf et al. argued, in contrast, that all taxa evolved at about the same rate, and that apparent discrepancies in the “genomic rate” of evolution among different taxa were artifacts produced by different levels of morphological complexity in different groups. Put simply, the paper argued that organisms with greater morphological complexity only look like they are evolving more quickly than simpler ones, because genetic changes are more readily expressed phenotypically in organisms with complex morphologies. Underneath, at the genomic level, “there may be a rather small range in rates of genomic evolution for different taxa over geologic time” (Schopf et al. 1975, 63).

Part of the reason previous analyses had missed this fact, the authors argued, was that it is extremely difficult to quantify and correlate degrees of “morphologic complexity” and “genomic change” in fossil organisms. In the first place, morphologic complexity is a subjective measure, and must be inferred as best as possible from imperfect fossil evidence. Secondly, rates of genomic evolution in fossils can only be estimated indirectly by guessing at how closely phenotypic change reflects underlying genetic variation. This presented a potentially circular argument: taxa that display slower rates of morphological change experience slower rates of genomic evolution because morphological change is an indication of rate of genomic change. Schopf et al. proposed to probe this relationship by employing the modified, morphological version of the MBL program used in Raup and Gould (1974) to produce cladistic lineages with 20 morphologic “characters.” They then applied Sepkoski’s QUAJAC cluster analysis program to group the lineages phenetically using four “stages” of morphologic complexity: 3, 5, 10, ... respectively. This produced four dendrograms, each of which associated the simulated lineages based on perceived degree of phenetic relatedness using a different number of characters (Schopf et al. 1975, 65).

The results of this simulation indicated that there was a direct relationship between the number of characters attributed to a group and its apparent rate of evolution. The four dendrograms were analyzed for survivorship, where the authors assumed that “short duration implies rapid turnover and rapid evolution,” and vice versa. They found that, plotted against an arbitrary time scale, the survivorship curve produced when clustering was based on 3 characters was twice as long as when it was based on 20. In other words, when greater morphologic complexity was taken into account, the lineages appeared to evolve “faster.” Ultimately, then, the paper argued that assumptions about inherent rates of genomic change needed to be recalibrated: organisms with less complex morphologies weren’t necessarily less evolved than more com-
plex ones. In fact, Schopf et al. suggested that average rates of genetic change (e.g., those involved in speciation) may be significantly higher for all taxa than had been commonly assumed, and that those rates were more or less constant throughout the lifetime of a lineage. One problem with this conclusion is that the fossil record appears to record frequent instances of rapid change followed by long periods of stagnation (e.g., punctuation and stasis). The traditional explanation for this pattern was that rates of genomic evolution are variable. However, the paper argued that this pattern could be explained via one of two alternative assumptions: in the first possibility, the rate of change is uniform, but phenotypic expression of genomic change decreases over time because of internal structural constraints. For example, “the structural limitations of frog morphology” allows less morphologic variation than mammalian morphology, which “allows a similar degree of genetic change to be translated into morphological adaptations in widely different environments” (Schopf et al. 1975, 67–68). In the second possibility, rates of evolution are proportionate to area available for colonization, and as environment fluctuates, so do opportunities for advantageous colonization by peripheral isolates with new morphological adaptations. In other words, populations are always experiencing the same rate of genomic change, but environment strongly determines whether those changes will be preserved as successful adaptations (Schopf et al. 1975, 68).

While the MBL group argued that the results of the simulation were important for reevaluating taxonomic practice, they concluded by connecting the paper to the broader project of investigating “equilibrium models in place of strictly historical explanations,” or taking a deductive approach to the fossil record: “Our emphasis on the role of stochastic processes over geologic time bears upon a much larger issue—what are the general implications for evolutionary theory if we are correct in claiming that genomic rates of evolution differ far less among major taxa than do rates of morphological change” (Schopf et al. 1975, 69). Although they admitted to being “not unanimous among ourselves regarding our favored guesses,” they presented two possible interpretations: the first, a “neutralist” view, held that the constant genomic rate of evolution was simply the result of “random fixation of mutations,” while the variation in rates of morphological expression was “merely the differential use of this genetic resource by the epiphenomenon of natural selection.” Though not directly attributed, this view would seem to be consistent with Schopf’s growing conviction that, at its root, evolution is primarily a stochastic process in which selective (individualistic, historical) factors play only a secondary role. On the other hand, the second interpretation spoke for Gould’s more traditional view:

1. that the genetic rate is primarily a function of the rate of speciation (viz. Eldredge and Gould, 1972),
2. that true rates of speciation among taxa differ far less than the differential propensities in various groups for parlaying large series of speciations into sequences that we recognize as evolutionary “trends” in morphology,
3. that genetic differences appearing at speciation are (nearly) completely controlled by natural selection (Schopf et al. 1975, 70).

Here, in short, were the two developing rival interpretations of the broader implications of the MBL simulation studies: Schopf’s vision of a “particle paleontology” which was ontologically stochastic and functionally non-Darwinian, versus the more restrained “heuristic” interpretation that preserved some measure of both historicity and of Darwinian evolutionary assumptions.

Real versus Random Clades

As the MBL group continued to explore more even more radical interpretations of the history of life, the community of evolutionary biologists’ reactions were mixed. E. O. Wilson, one of the referees for Paleo-biology for the 1975 Schopf et al. paper, gave the manuscript an unequivocally positive review. In rating the paper “excellent” and “acceptable with little or no revision,” he described it as “an absolutely first-rate paper, of fundamental importance,” and he complimented the authors for having “fashioned an essentially new basic idea fully” (Wilson, review of “Genomic versus Morphological Rates of Evolution,” 29 July 1974: PS-P 4). The MBL group also received friendly publicity in the form of a “Research News” column in a 1975 issue of Science, which gave a detailed summary of the papers up to that point and described the work as “arousing a great deal of interest among paleobiologists” (Kolata 1975, 625). While the essay did note paleontologist Arthur Boucot’s assessment that the model was “clever, polished, but of limited use,” it undoubtedly brought the project welcome attention from a broader audience (Kolata 1975, 660).

A less friendly response, however, was published the following year
in *Paleobiology*, when Niles Eldredge challenged the conclusions of the paper on genomic rates (Schopf’s frosty editorial handling of this piece was discussed in the last chapter). In arguing that the simulation approach “obscured some probably real biological phenomena of great theoretical interest,” Eldredge questioned the basic logic of the 1975 paper’s conclusion that genomic rates are constant (Eldredge 1976, 174). If, he argued, we assume that most genetic change occurs through geographic variation, genome sampling in isolated populations, and character displacement, then the better question would be “Is there variation in rates of speciation among different kinds of organisms?” He then argued—using as examples both the “living fossil” *Limulus* and a comparison between clams and mammals—that disparities in evolutionary rates are real and that Schopf et al. were wrong to minimize the importance of geographic and environmental influence on local populations, and he admonished the authors to restore their discussion of evolution to “the language of evolutionary and ecological theory” in which “‘population’ and ‘species’ are the core words” (Eldredge 1976, 177). Gould’s immediate response in the same issue of *Paleobiology* confirmed that Eldredge had scored a direct hit: while Gould defended what he called “the Lyellian tradition of probing ‘behind appearances,’” he nonetheless conceded that Eldredge’s argument that questions about genomic evolution ultimately reduced to questions about speciation was one with which he “can scarcely disagree” (Gould 1976a, 177). That there were pronounced differences in rates of speciation among different taxa was a foregone conclusion. The question was how to interpret those differences.

Gould then summarized the strong and weak interpretations of the MBL model as he saw them (which correspond to what I have described as the “ontological” and “heuristic” interpretations of the stochastic null hypothesis) and admitted that in his view the 1975 paper supported only the weak version, although “some of its authors (not including myself) believe or at least prefer” the strong one. Then, in a particularly candid and revealing passage, Gould articulated for the first time (at least in print) what would become one of the central metaphors in his own, emerging view of the history of life:

> Are the profound differences [in rates of speciation between Coelacanthini and Coleoptera]... a determined result, predictable *a priori* from the intrinsic biology of the two groups? Or is the difference a complex result of stochastic opportunity and a different number of founding lineages...? In other words, if we could replay the tape of life, might coelacanths become the terrors and beetles the monoplacophorans? In short, empirical differences in rate of speciation exist—how could it be otherwise in a non-typological world. But we must know whether these differences are essentially random scattering about a mean rate (the [genetic] metronome hypothesis) or a determined and predictable feature of certain morphologies and environments.

Here, in short, was the central question: Is evolutionary change essentially a historically determined, contingent process, or is it rather a random walk? Gould confessed that while his “own intuition leads me to Eldredge’s conclusion—that the differences are predictable consequences of functional anatomy and environmental space,” he nonetheless concluded, “I cannot vindicate this intuition with any satisfactory data” (Gould 1976a, 178). Thus, in his response to Eldredge, Gould found himself torn between conflicting loyalties: on the one hand, to his co-author Eldredge and their “literal” reading of the fossil record as a sequence of historically contingent events, and on the other to his co-author Schopf, and to their reading of the record as an idealized statistical record of stochastic fluctuations around an equilibrium.

Despite mounting disagreements, the MBL collaboration produced one last major paper, “The Shape of Evolution: A Comparison of Real and Random Clades” (Gould et al. 1977). This paper revisited the original 1973 *Journal of Geology* study but provided an expanded comparison with clade diagrams derived from real taxa. As such, the technical aspects of the paper followed a by now familiar procedure: First, clade diagrams were generated using a modified version of the original MBL program. Next, the size and shape of the simulated diagrams were measured and tested to determine frequency distributions, or “clade statistics” for the simulated clades. These clade statistics measured the size, maximum diversity, duration, center of gravity, and extent of fluctuation for each clade. As in earlier studies, a “damped-equilibrium” function was built into the program, which was justified as a representation of the MacArthur-Wilson insular equilibrium model. In the final stage, the paper computed clade statistics for 144 orders, 206 families, and 1442 genera of actual fossil organisms, derived primarily from the *Treatise on Invertebrate Paleontology* (Gould et al. 1977, 30). Clade statistics for real and simulated clades were then compared in order to identify features of real clades not found in random ones. The computations were mostly performed by Sepkoski, who wrote a FORTRAN program that calcu-
lated and plotted clade statistics. Sepkoski was therefore added as a fifth author, in a departure from the “quadripartite” scheme debated by the MBL group.

The paper itself was written primarily by Gould, who prefaced the technical sections with a fairly extensive meditation on the meaning of the stochastic simulation “experiments.” He explained that while the authors did not necessarily assume “that life’s history is ontologically random,” the stochastic null hypothesis was an effective “criterion of subtraction” for ascertaining what amount of apparent order requires no deterministic cause” (Gould et al. 1977, 23–24). As Gould explained in the introduction, though, the paper also had a “larger, ulterior motive”:

We believe that paleontology—the most inductive and historical of the sciences—might profit by applying some deductive methods commonly used in the non-historical sciences (without sacrificing its important documentary role for the history of life). We may seek an abstract, timeless generality behind the manifest and undeniable uniqueness of life and its history (Gould et al. 1977, 25).

Gould acknowledged the debt this approach owed to “the other branch of natural history most celebrated for the complexity and uniqueness of its subject—ecology,” and also defended a version of the species-as-particles idea where “untimebounded” and “untaxonbounded” models “treat all times and taxa alike” (Gould et al. 1977, 25).

Nonetheless, in important ways this paper did not pursue the more radical, ontological interpretation of randomness in the history of life. Despite the fact that the comparison between real and random clades appeared to indicate “the outstanding feature of real and random clades is their basic similarity,” the paper concluded by highlighting three significant departures from randomness in the real clades. In the first case, the study found that living clades tend, in the “real world,” to be significantly larger than extinct ones. While the paper discussed possible sampling biases which might produce this phenomenon, the authors nonetheless concluded that “a plausible story in the deterministic mode” may offer the best explanation: “The real world is ‘taxonbound’—superior designs tend to persist, diversify, and survive” (Gould et al. 1977, 34). In the second instance, the extent of fluctuation of diversity—measured as the “uniformity” (UNI) of a clade—was much higher in certain real clades than in any of the simulated ones. Low values of UNI—meaning fairly significant fluctuations of diversity in a taxon—were found especially in amphibians and mammals, and the authors were unsuccessful in adjusting the parameters of the simulation to produce random clades with similar values. Furthermore, fluctuations in diversity among different groups appeared to be correlated in time. Again, the authors concluded that this may “represent a non-random effect,” as a result of “real, biological interaction” between groups. Thus, “the real world may be, in this respect, ‘timebounded,’” meaning that “some times really are ‘good’ for certain groups” (Gould et al. 1977, 37). Finally, the comparison also found that the average “center of gravity”—“a measure of the relative position in time of the mean diversity”—was lower for extinct clades among the real sample than in the simulation. This effect was especially pronounced for early clades of the Cambrian-Ordovician period of rapid evolutionary expansion, where clade shapes in groups such as trilobites, brachiopods, and nautiloids tended to have clade shapes that were wide at the base, well before the midway point in the groups’ chronology. The “deterministic” explanation for this effect was that “an average real clade tends to be wide at the bottom because it radiates rapidly following the invasion of new ecological space or the evolution of new morphological designs by ancestral lineages;” then achieves optimal diversity before tapering off very slowly towards extinction. While the authors explored a variety of ways in which such a pattern could be accounted for in the simulation, they also frankly admitted it posed a potential “violation” of the stochastic model by suggesting that “all times are not alike to members of a clade if chances for diversification are characteristically greater during their early history” (Gould et al. 1977, 38).

All in all, these limitations in the random model can be interpreted as an endorsement of the heuristic value of the stochastic null hypothesis. In this paper, the “criterion of subtraction” appeared to work very well for separating those patterns in the history of life that did not require deterministic explanations from those which did. One such case, it would emerge, was mass extinction, which was explicitly acknowledged to be outside of the testable parameters of the MBL model. And despite the confident spin with which the paper concluded—calling for a revival of Charles Lyell’s dynamic steady-state model of the history of life that rejected directionalism and progress—it is no coincidence that this paper would be the final entry in the MBL collaboration. One could argue that, with this study, the MBL model had simply run its course.

As we will explore below, it may also be that this final paper exacer-
bated the growing divisions within the group over how to interpret the model. As primary author of the 1977 paper, Gould presented his own more moderate heuristic interpretation, but Schopf, in particular, was becoming ever more attached to a radical, ontological interpretation of stochasticity. It is also the case that the 1977 paper brought more uncomfortable critical scrutiny to the model than had any of the previous efforts. The manuscript was initially submitted to *Science*, where it was rejected after several lukewarm reviews. One referee commented that the paper was “not important enough to warrant publication as a lead article in *Science*,” and felt it was overly long and wordy. This view was echoed in other reviews as well, and while the most positive found the paper “generally excellent and stimulating,” the most damaging report contended that the paper’s “results have no explanatory significance.” This last review, which was unsigned, was the most strongly worded, and Gould speculated that its author was “GGS himself—I’d know his style (& typewriter) anywhere” (PS-P “1977”). This reviewer—George Gaylord Simpson or not—chastised the authors for confusing the terms “random” and “stochastic,” and criticized the ambivalent stance they took on the implications of randomness for evolution, noting that while “there is some implication that the ‘real’ distributions studied are acausal . . . [which] would be a revolutionary doctrine not only for evolution but for science in general . . . no such conclusion is really inherent in their results.”

This paper also generated the most damaging published criticism of the MBL model. These criticisms centered on improper scaling in comparisons of real and simulated clades in both the original 1973 paper and in the 1977 follow-up, and were first presented by Steven Stanley in his 1979 book *Macroevolution: Pattern and Process* (Stanley 1979, 279). Stanley’s basic argument was that the similarity in shapes between real and random clades was artificially enhanced by the comparatively low numbers of taxa composing each of the random clades. In other words, the random clades consisted of far fewer units than average real higher taxa, which gave them artificial instability and made them much more likely to rapidly diversify via random branching and extinction. In 1981, Stanley coauthored a paper in *Paleobiology* that reiterated this point and argued that species, rather than genera or higher taxa, were the appropriate units for simulation (Stanley et al. 1981). While the reaction from the MBL group was initially quite defensive—leading to an acrimonious exchange between Stanley and Schopf over the paper’s publication—Stanley’s criticisms have for the most part been vindicated. As Raup acknowledged years later, “They were bang on—they were dead right” (Raup interview).

**The Demise of the MBL Group**

**Schopf versus Raup: Determinism and Extinction**

Up through the 1977 paper on clade shape, the MBL group had successfully, if sometimes uneasily, juggled its various allegiances and interpretations. However, internal disagreements would soon lead to tensions that ultimately ended the collaboration. A particular locus of conflict was the proposed stochastic methods primer, on which Schopf began to fixate as a vehicle for proselytizing his view of stochastic paleontology. Raup had been tasked with bringing an outline to the December 1973 meeting, an arrangement that made sense given the fact that Raup was most intimately knowledgeable about the workings of the simulation models. However, even as he accepted this task he worried that “it [the book] might turn out to be more of a swell loopy than a fell swoop” (Raup to Schopf, 20 November 1973: Schopf pap. 3, 30). Apparently Raup was not encouraged by conversations that took place at Woods Hole, because in his next communication with Schopf on the subject—more than a year later—he announced, “I have been doing a lot of thinking about my role in the enterprise and have finally decided to opt out” (Raup to Schopf, Gould, and Simberloff, 7 April 1975: Schopf pap. 3, 30). Raup explained that his “negative feelings about the venture have been aired at length” during the 1973 Woods Hole meeting; nonetheless, he left the door open for future collaboration, and gave his “complete blessing and cooperation” to Schopf and Gould to continue the manuscript without him. Although the letter did not elaborate what those “negative feelings” were, Raup recalls experiencing a growing concern that Schopf’s aggressive promotion of stochasticity and “gas laws” might have an alienating effect on more traditional paleontologists, and a fear that “Tom’s messiah approach to the whole thing” might undermine the positive potential of the MBL collaboration (Raup interview).

Raup’s concern must have gotten through to Schopf, because the next time Schopf broached the book with Raup and Gould, his tone was considerably more restrained. He explained that in “considering why it is the MBL work does not receive the credit it is due in the profession,” he
realized that the group had not sufficiently articulated to the profession how their approach contributes to the “day to day activity” of traditional paleontologists and geologists. After all, Schopf admitted, since “the primary concern of geologists is the explanation of particular events,” and “what we have done does not (generally) relate to events,” it was hardly surprising that “our colleagues look at what we have done and say ‘so what!’” (Schopf to Raup and Gould, 30 August 1977 [draft]: Schopf pap. 3, 30). “It matters not one iota that species may be particles like atoms” Schopf continued. “After all, the blastoids went extinct didn’t they . . . and that is what needs explaining—not some fancy footwork about how some group went extinct, and it ‘happened’ to be blastoids.” The solution Schopf proposed was to find a way to “provide bridges” between traditional paleontological questions and random models, in which case it was incumbent on the MBL group to “be able to provide a prospectus of what are the interesting questions which is both attractive and within the capabilities of the guy who was previously worried about why the blastoids were done in.” For that reason, he said, “a book-length treatment is desperately needed” because “only in that way will the full panoply and inherent richness of the stochastic models approach become apparent.”

Schopf then outlined an approach in which questions about particular historical events could be redefined so as to preserve their legitimacy, but “in such a way that we also provide an answer—nontraditional to be sure” for why stochastic models were relevant to those questions. One strategy was to argue that “specific causes are so multifaceted and unable to be sorted out” that continuing to search for individual, deterministic answers to questions like ‘why did a particular group become extinct’ was futile. In other words, here Schopf was advocating the weaker, heuristic MBL interpretation, in which stochasticity was most effective as a null model, and proven statistical techniques like survivorship analysis gave insight into specific paleontological problems. “By far our best strategy,” Schopf concluded, is “to encompass and conquer. But if we do so, we need to treat the traditional problems of paleontologists. Thus our taking-off points start with a real world problem. Every chapter in the book should have as its first sentence the statement of a specific problem the day-to-day paleontologist meets with—and can relate to. We need to do the extra work of going more than half way, or so I feel” (Schopf to Raup and Gould, 30 August 1977 [draft]: Schopf pap. 3, 30).

The final suggestion Schopf made was that the book project be put on hold—temporarily—in favor of offering a workshop on stochastic models in order to provide “feedback to see how things can best be done.” Schopf’s change of heart encouraged Raup to put aside his reservations and participate, and the two began collaboration on a short primer for the workshop (funded by the National Science Foundation), which they envisioned as a rough first version of the eventual book. Raup wrote an initial draft, and plans went ahead to present a workshop on stochastic models at the National Museum of Natural History in early June 1978. A few days before the workshop began, Schopf proudly sent a revised copy of the primer to Gould. “I am rather pleased with the way this is developing,” he commented, asking Gould to consider writing a “major Preface” for the published version. Schopf suggested that “such a forward [sic] might be historical, might be ‘idiographic’ and ‘nomothetic’ with regard to paleontology, and would be acknowledged on both the dust cover and the title page as ‘Preface by Stephen Jay Gould’” (Schopf to Gould, 2 June 1978: Schopf pap. 5, 14).

Unfortunately, Schopf badly misjudged Raup’s reaction to the draft. A month later—and after the workshop concluded—Raup sent Schopf what must have been a deflating letter in which he spelled out reasons why he was “not optimistic about the primer at this point.” Chief among Raup’s concerns were “technical faults and omissions [sic] which will require a lot of work to remedy,” and an impression that Schopf had deviated from the more moderate approach outlined in his earlier letter. As Raup explained,

Our basic objective has been to produce a ‘how to’ treatment of certain techniques of paleontological importance. We have not had in mind the presentation of a definitive theory of macroevolution. . . . We wanted to produce a book that would be used by everyday paleontologists on everyday problems—not necessarily confined to those in evolutionary theory. I am afraid we have misfired: the techniques answering the above requirements are few and far between and there is (I think) much too much theory mixed in (Raup to Schopf, 17 July 1978: Schopf pap. 3, 30).

Following a chapter-by-chapter enumeration of technical and conceptual faults in the draft, Raup concluded that Schopf’s revision “has indeed moved you away from the primer objective” and warned “if we publish a book in something close to its present form, we will be absolutely crucified by friend and foe alike!”

Despite declaring “little faith in the present attempt,” Raup closed his
letter with an attempt at finding a constructive solution. He agreed that “we would all like to put what we have learned from the MBL project in some sort of hard-hitting book form,” and suggested “a different tack”: We have written a lot of MBL papers. They have gained considerable attention and have started a lot of argument. Two of the papers were in semi-popular journals and there was the commentary in *Science*. . . . As a result of all of this, I suspect that there are relatively few of our paleontological colleagues who remain unaware of the MBL work. This means to me that a book version must really be stronger than the sum of its parts. If it isn’t, it is a waste of the reader’s time. A collected reprint volume would do as well (Raup to Schopf, 17 July 1978: Schopf pap. 3, 30).

The solution he proposed was for Schopf to take the project in his own direction, since “what you are trying to do calls for a totally different format.” Raup imagined that the book would present “a clear statement of the species-as-particles idea” through rigorous testing and documentation of a specific set of models. However, he concluded that this would be “a tough job,” and stressed that he did not see a role for himself in such a project.

Gould had been on the sidelines during much of this discussion, but after receiving both Schopf’s invitation and Raup’s response he sent Schopf a letter in which he attempted to play peacemaker. On the one hand, he reasoned, Raup’s objections put further progress on the project in jeopardy, and suggested “I’d do best by just holding on to the ms. for a while until the dust clears.” On the other, he tried to reassure Schopf of his ultimate support: “let me reiterate my agreement with you that such a document represents a consistent, logical, and forceful next step and that our major task in pushing our view” (Gould to Schopf, 7 July 1978: Schopf pap. 5, 14). Essentially, Gould left the decision about how to proceed to Schopf, but stressed his willingness to contribute the invited preface “once we all clarify and agree.” Schopf replied a week later to express ‘appreciation for Gould’s support and ‘puzzlement’ at “the Raup situation.” He rather breezily waived aside Raup’s hesitaton as the result of Raup’s “very high aspirations for the National Academy,” and advanced a “theory” that Raup might feel threatened by a co-authored project which would “steal his thunder and dilute the impact of his work.” “Fearing that,” Schopf continued, “and wanting the NAS recognition, he may feel very uneasy about doing anything as major as this with coauthors. If so, we’d better get him elected as soon as possible so that the business of remaking paleontology can progress as rapidly as possible” (Schopf to Gould, 30 July 1978: Schopf pap. 5, 14). Schopf made no comment about any of the substantive criticisms or suggestions Raup had raised, but promised to revisit the matter after he had spent time with Raup in Chicago.

At least initially, Schopf seems to have believed that his differences with Raup could be patched up. In a letter to Raup in late December 1978, he reiterated his continuing “belief of the importance of the stochastic paleontology” and stressed his view of the importance “of a primer which has this theory at its core.” He even optimistically closed his letter by mentioning that he “look[ed] forward to reading a revised draft of either the book or the primer when I return [from a semester in Germany] at Christmas!” (Schopf to Raup, November 1978: Schopf pap. 3, 30). However, this cheerful optimism could not prevent further disintegration of the collaboration, and in early 1979 Raup sent Schopf a long, philosophical letter that highlighted the widening gulf between the two.

At the time of this letter, January 1979, Raup was experiencing a radical change in his views about randomness and determinism. Over the several years that had passed between the publication of the first MBL paper, in 1973, and the paper on clade shape in 1977, Raup’s interpretation of the role of stochastic processes in nature appears to have remained fairly consistent. Raup’s own recollection about his original attitude in 1973 is fuzzy, but Simberloff recalls that “of the group, I felt at the time that Dave was almost, but not quite, committed to the view that many things that were interpreted as having a very specific cause were in fact random, at least with respect to that putative causal factor” (Simberloff, e-mail communication with John Huss, 11 March 2002). Raup acknowledges that his 1974 morphology paper with Gould reflects an interpretation in which “random processes often produce patterns that APPEAR to be worthy of deterministic interpretation,” and it seems likely that he was one of the authors to whom Gould alluded, in 1976, as supporters of the “strong version” of MBL (Raup, e-mail communication with John Huss, 13 March 2002). In the same year that the final collaborative MBL paper was published, Raup also wrote an essay for *American Scientist* entitled “Probabilistic Models in Evolutionary Paleobiology,” which advocated a version of the more radical, ontological in-

2. Raup was indeed elected to the National Academy in 1979.
in summarizing the advances of the MBL model for a semi-popular readership, Raup explained that specific causes for changes such as faunal succession may be viewed as the result of random fluctuations in a Markov chain, and he drew explicit attention to the possible conclusion that “natural selection may behave (mathematically) as a random variable.” While he acknowledged that describing “such changes as ‘random’ does not deny cause and effect,” he stressed that “the distribution of these causes in geologic time may be essentially random,” and concluded that “evolution certainly should be viewed in a Markovian framework” (Raup 1977, 51).

Nonetheless, as Raup recalls, by the time of the 1978 workshop, he was ready to concede that “the external rare event was deterministic . . . [and] I became more and more convinced that the externalities were important” (Raup interview). This brings us back to Raup’s letter to Schopf, which began with a meditation on the consequences for the profession “if you and I and Steve really succeed in selling our current brand of nomothetic paleontology.” He imagined that “scores of young paleontologists will be plotting survivorship curves (or whatever) in a slavish and unthinking manner and much of the work will have to be thrown out ultimately” since “the scientific work that is done will probably be more wrong than right” (Raup to Schopf, 28 January 1979: Schopf pap. 3, 30). After all, he reminded Schopf, “Every generation of paleontologists has had its nomotheticists.” Nonetheless, taking “a more positive stance,” Raup asserted his firm conviction “that the current stochastic models are right—at least at some scale.” The problem, he argued, was determining the appropriate scale.

Quickly, however, Raup revealed that a subject that would come to occupy much of the remainder of his professional career—the interpretation of mass extinctions—had largely precipitated ...

... more convinced that the key gap in our thinking for the last 125 years is the nature of extinction.” He went on to argue:

If we take neo-Darwinian theory at face value, the fossil record makes no sense. That is, if we have (a) adaptation through natural selection and/or species selection and (b) extinction through competitive replacement or displacement, then we ought to see a variety of features in the fossil record that we do not such as: (a) clear evidence of progress, (b) decrease in evolutionary rates (both morphologic and taxonomic), (c) possibly a decrease in diversity

(at least within an adaptive zone). Now we do not see these things because: (a) we are too dumb, or (b) the record is lousy, or there are features of the evolutionary mechanism that prevent the approach to a steady-state.

Raup explained that his “candidate explanation is, of course, that extinction is random with respect to fitness. By this scenario,”

the neo-Darwinian system is at work all the time—producing trilobite eyes and pterosaur flight—but never really gets anywhere in the long run because the trilobites and pterosaurs get bumped off (through no fault of their own!).

. . . The system is always heading toward a steady state but never gets there (Raup to Schopf, 28 January 1979: Schopf pap. 3, 30).

So far, Raup’s view was consistent with Schopf’s vision of an evolutionary process held in check by stochastically varying fluctuations in extinction rates around an equilibrium. Extinction is not a matter of bad genes, in a Darwinian, selective sense, but rather bad luck.

The problem with this more radical view, Raup confessed, is that there was simply too little “convincing documentation” to support it, making it “nothing more than a just-so story.” What was required were studies of actual groups in the fossil record in which extinction could be shown to be nonselective. Take, for example, the trilobites, whose abrupt departure in the Permian is one of the most spectacular examples of extinction in the fossil record. “By my grand scenario,” Raup explained, “the demise of the trilobites was just bad luck on their part”; in other words, the extinction rates of trilobite taxa were no different from those of other groups, but trilobite diversity simply had the ‘misfortune’ to “wander down to zero over the course of a couple of hundred million years.” Unfortunately, Raup admitted, he no longer believed such a scenario was mathematically plausible. According to standard equilibrium assumptions from island biogeography, speciation rates ($p$) and extinction rates ($q$) should be roughly equal for all species over the Phanerzoic (in order to prevent either total extinction or exponential expansion of life). Using accepted values for $p$ and $q$ of 0.1 per million years, and assuming that approximately 1,000 trilobite species existed at the height of the group’s diversity, then the probability that any one of the 1,000 species would become extinct over the 200 million year existence of the group is 0.95. To put it in terms of survivorship, roughly 1 in 20 trilobite species should have had living descendents at the end of the Permian.
However, Raup pointed out, the real question was the probability that all of the 1,000 species would become extinct. This can be expressed as the extinction probability (95%) multiplied exponentially by the number of species ($0.95^{1000}$), which yields the astronomically low probability $5 \times 10^{-23}$, or $0.0000000000000000000005$. “In other words,” Raup concluded, “the chances are nil that the trilobites could have drifted to extinction and one must conclude that there must have been something different about their extinction rates” (Raup to Schopf, 28 January 1979: Schopf pap. 3, 30). Or, to put it another way, trilobites would have to have had extinction rates an order of magnitude greater than other groups’ in order for their total extinction to have been plausible. In either case, the assumption that extinction is non-selective was in serious jeopardy: there must have been something special that made the trilobites candidates for complete extinction. If this was true, Raup reasoned, the “Paleozoic extinctions [appear to have been] actually selective . . . meaning in turn that trilobites were inferior beings and deserved to die.” And he closed the letter with the candid admission that “if I were to be completely objective . . . I would have to conclude that the stochastic model does not apply to the distribution of species extinctions between and among classes or phyla,” which led to “a purely Darwinian conclusion.” His final caution to Schopf was, “I don’t think it is wise or fair to present [the stochastic model] as the final solution until it can be proven rigorously” (Raup to Schopf, 28 January 1979: Schopf pap. 3, 30).

Schopf responded with a long letter in which he attempted to sway Raup with an argument about survivorship curves, claiming “the Raup paradox” was “fallacious” since it implied “that NO GROUP the size of trilobites could ever go extinct” (Schopf to Raup, 8 February 1979: Schopf pap. 3, 30). Of course, the obvious rejoinder was that Raup’s proposition was a paradox only if one insisted on viewing extinctions as nonselective and randomly distributed through time. If, on the other hand, one rejects either of those assumptions—admitting either that some groups have bad genes or that historical events like mass extinctions have determinate causes—then Raup’s calculation appears to be fairly damning evidence against the stochastic, species-as-particles view. But by this point Schopf had become even more committed to an ontological interpretation of the MBL model; as he explained to Raup, “In my view, all of paleontology, i.e., all of those fossils, is (are) simply a metaphor [sic] for what is really the statistical mechanics of a series of interacting hollow curves.”

Schopf’s statement can be interpreted as the most extreme application of the idealized metaphor for reading the fossil record: in his view, the fossils themselves are a “metaphor” for the model, implying that the statistical idealization itself which is the true “text.” Schopf’s commitment to this extraordinary interpretation was, by this late stage, inflexible and dogmatic: his commitment to nondeterminism prevented him from seeing Raup’s probability calculation as a legitimate obstacle to the stochastic view, because he refused a priori to admit alternative mechanistic explanations (such as inherent maladaptiveness or historically contingent and extrinsic causes of mass extinction). Raup obviously recognized this, and in his next letter he confided to Schopf, “On a somewhat serious note, your recent letters have given me some concern. Could it be that you are getting a bit carried away by stochastic approaches to paleontology? I fear that you will lose your credibility if you press the gospel too hard. My concern is difficult to express. I am sure you are more inhibited in ‘public’ than in personal letters but the message that comes through the letters is that you have found the Holy Grail and that anyone who does not recognize this (and join in the feast) is a poor slob in desperate need of salvation (Raup to Schopf, 22 February 1979: Schopf pap. 3, 30).

He went on to warn Schopf that this attitude might well end with Schopf as “the ultimate loser,” and even raised the specter that Schopf could “join the ranks of T. Y. H. Ma, Petrunkovitch, Meyerhoff, Goldschmidt, et al. . . . [all of whom] lost credibility and thus lost the ball game.” “All I am asking,” Raup concluded, “is that you (1) think hard about your modus operandi, and (2) think hard about just how compelling the case is for our particular breed of stochastic paleontology.”

Schopf versus Gould: Replaying the Tape of Life

At around the same time, Gould finally voiced his own concerns about Schopf’s increasing attachment to the ‘species as particles’ view of paleontology. At the time of his last exchange with Raup, Schopf was putting the final touches on an essay that would appear in *Paleobiology* in late 1979 entitled “Evolving Paleontological Views on Deterministic and Stochastic Approaches.” Despite the seemingly neutral title, the paper was a polemical statement of Schopf’s grand vision for stochastic paleontology, and opened with the declaration that chance and stochastic pro-
cesses form “the first order pattern of organization of the history of life” (Schopf 1979, 337). As an introductory analogy, Schopf drew on historian Herbert Butterfield’s 1931 classic The Whig Interpretation of History, which he extrapolated to an argument “that Whig values are not limited to human history but are found in a pervasive way in interpretations of the history of life,” in which evolutionary “progress” is interpreted as the result of a causally determined, directional process (Schopf 1979, 338). In place of “the extraordinarily strong reliance on determinism in paleontology,” Schopf explained that

the proper type of theory to apply to large statistical summaries is some form or another of stochastic theory, such as occurs in chemistry (the gas laws), population biology (demography), and physics (the Heisenberg uncertainty principle). The fate of any given molecule, or individual animal, or atom is of no concern per se. Rather, the ensemble statistical properties of the particles and the types of predictions which those properties allow are what is of interest.

While he stressed that such a view did not ignore particular historical events, he nonetheless asserted that “the incorporation of stochastic thinking into paleontology does say that there was nothing inevitable either in evolution or in history that a priori determined either the present state of affairs, or any specific past configuration” (Schopf 1979, 343).

Schopf then applied this insight to two major topics of paleontological interest: rates of speciation and extinction. In the first case, he essentially recapitulated the argument of the 1975 MBL paper that different taxa have inherently different rates of genetic evolution. However, he departed from the 1975 paper by steering the discussion to a critique of the “philosophical assumption” that “a literal reading of the objects which comprise our fossil record is assured to reflect a ‘true’ image of a previous reality” (Schopf 1979, 344). In fact, Schopf maintained, such a “literal reading” gives “a grossly distorted view of rates of evolution,” and paleontologists would be better served by taking a more idealized, statistical view of the record (Schopf 1979, 345). In the second case, Schopf reiterated the criticism he had expressed privately to Raup about fallacious attribution of selective causes to extinction, which practice he termed “tautological” since it depended (he argued) on a post hoc determination of ‘fitness’ based merely on the record of which species did and did not survive. “‘Fitness’ or ‘adaptation’ may not have been a factor” in extinctions, Schopf contended, “unless one defines them to have been a factor. In a world of fixed total resources that fluctuates from time to time and place to place, where individuals cannot live forever, it may be no more than bad luck as to which species persist, or die” (Schopf 1979, 346). Schopf concluded the essay with a seven-point outline of a “stochastic view” that mixed elements of biogeographic equilibrium theory with precepts of the MBL model. In point 5—that rates of extinction and origination are random with respect to membership in a particular taxonomic group—Schopf paraphrased (without attribution) Gould’s “tape of life” metaphor, observing that if we were to “replay geologic history within the same general ecologic constraints as have prevailed . . . it could be that (for example!) blastoids live through the Permian, and crinoids die out” (Schopf 1979, 348).

When Schopf sent Gould a draft of this essay just prior to publication, Gould made a comment that, in many ways, epitomizes the growing distance between his own and Schopf’s understanding of the role of chance and determinism in historical processes:

You continually confl ate (though they are not unrelated of course) the notions of predictability and stochasticity. Stochastic models can, of course, lead to a high degree of predictability, at least for general patterns of events. Of course I agree that the most fascinating aspect of life on earth is that it would probably play itself out in a totally different way if we started again from the same initial conditions—but this metaphysic (which I share with you) is not the essence of maintaining a stochastic perspective in paleontological theory (Gould to Schopf, 25 June 1979: Schopf pap. 5, 59).

As Gould was implying, sensitivity to initial conditions in fact presupposes determinism, since while the initial state of a system may be unpredictable, subsequently unfolding events can, as Gould noted, be quite predictable. Gould was also drawing attention to two alternative interpretations of the metaphor “replaying the tape of life.” By 1979, Gould’s interests were in the midst of a slow turn back to one of his original preoccupations: the role of physical developmental constraints in evolution. This was heralded by the publication of his first book, Ontogeny and Phylogeny, in 1977, which combined a historical and scientific reexamination of Ernst Haeckel’s intuition about parallels between embryonic development and evolutionary history (Gould 1977).
“Towards a Nomothetic Paleontology”

Paleobiology in which Schopf’s essay appeared also contained a paper, coauthored by Gould (along with David Wake), entitled “Size and Shape in Ontogeny and Phylogeny,” which drew attention to the relationship between the timing of developmental stages and morphological evolution, and which is now considered one of the early contributions in the field of evolution and development, or evo-devo (Alberch et al. 1979). Finally, 1979 was the year that Gould and Richard Lewontin published their famous critique of adaptationism, “The Spandrels of San Marco,” in which they emphasized the role of nonselective or accidental by-products of evolution (“spandrels”) in contributing to—and constraining—the evolution of organic forms (Gould and Lewontin 1979).

In other words, Gould’s own distinctive view of life was experiencing significant change at exactly the time when Schopf showed him his essay on stochastic paleontology. In Gould’s developing view, stochastic processes were balanced by three important kinds of constraints. The first was intrinsic structural factors like allometric relationships that limit or direct morphology along particular pathways. This notion of constraint harkened back to Gould’s early interest in D’Arcy Thompson’s “laws” of form, and while it was essentially nonselective, it did consider form to be in an important sense determined by the laws of geometry. The second kind of constraint was the influence of developmental pathways in ontogeny and phylogeny. The essential idea was that certain directions, once taken, were irreversible: organisms with bilaterally symmetrical appendages radiating from an axial notochord may not have been in any sense evolutionarily “necessary,” but once that particular “choice” was taken by natural selection, certain morphological options were closed off to further exploration. The final kind of constraints Gould recognized were geological and environmental factors: he argued that the history of life was shaped by particular, distinctive historical events that are independent of normal Darwinian processes. For example, Gould would become quite interested in the role of extraterrestrial mechanisms for mass extinctions, which periodically reset the adaptive conditions of the physical environment in unpredictable ways. Each of these senses of constraint contributed to what Gould would famously define as “contingency” in the history of life: the interaction between unpredictable or random events, and the consequences of those events, which were in an important sense deterministic. He would explore this idea at length in his 1989 book Wonderful Life, and also in his work with Elizabeth Vrba on macroevolutionary hierarchy and “exaptation.” The crucial idea in both cases was that we live in “a world built by irrevocable history” (Gould 1989b; Vrba and Gould 1986, 226).

The message Gould took away from the MBL model, then, was subtly but importantly different from Schopf’s. Gould was impressed by the way random processes could generate apparent order, but was not ready to give up a “literal” reading of the fossil record. The “tape of life” metaphor was a lesson about sensitivity to slight differences in initial conditions, and Gould realized that determining which particular outcome resulted in the end was a matter of “irrevocable history.” The fact that it was precisely these contingent factors that gave history its particularity—such as major mass extinctions—that the MBL simulation did not take into account was something Gould frequently acknowledged (Gould 1978, 279). Schopf, on the other hand, saw the MBL model as a lesson that the history of life could be interpreted in such a way that all particularity was ignored—in a sense, it allowed history without historicity. This helps to explain Schopf’s adamant objection to two ideas Gould championed: punctuated equilibria and catastrophic mass extinctions. Schopf consistently rejected the notion that mass extinctions have deterministic, identifiable causes out of hand. He argued, for example, that the great Permian extinctions were a consequence of the slow shifting of continents and the MacArthur-Wilson species-area effect, and he campaigned against the theory that dinosaurs became extinct as a result of a bolide impact up until his death in 1984 (Schopf 1974).

As for punctuated equilibria, Schopf best expressed his view in a letter to Gould in 1981, in which he related his social views to his philosophy of science:

I was struck again—and not for the first time . . . that the social level was far more important than the talents of any individual. And if so for Homo sapiens . . . then it must be the case for all species. The luck of the draw is the dominant factor in how we live our lives—mostly by how it constrains the opportunities before us.

Now, if one has this sort of a social view, it seems to me that “stochastic” paleontology flows effortlessly—it agrees with a luck of the draw view of life. . . . This being so, it is now completely unacceptable to me that any species is really any different from any other species. They are all out there trying like hell to do well. Sure, God helps those that help themselves. But what does God do when all species are helping themselves?? The traditional view
is that, under these circumstances, God is picking and choosing! But surely that is nonsense.

So where does that leave one? Well, it leaves me thinking there must be something wrong with Raup’s conclusion that trilobites are morally degenerate (or at least that they couldn’t have gone to extinction by mere accident!). . . . If all species through time are equally “successful”—and if all species at any given moment in time are equally successful—then the notion of “success” (sensu latu) has no place in evolutionary theory (Schopf to Gould, 4 December 1981: Schopf pap. 8, 31).

This view conflicts in one important way with Gould’s: While Gould might have agreed that “success” was a problematic term when applied broadly to the history of a lineage, his contingent view of history rejected the argument that all organisms were, at any particular time, equally prepared for certain environmental conditions. If one accepts that unique events—a bolide impact at the Cretaceous-Tertiary boundary, for instance—play a role in the history of life, as Gould did, then one accepts that, even if for no fault of their own, some organisms (dinosaurs) failed while others (mammals) succeeded in meeting the new conditions that resulted.

However, Schopf’s “species-as-particles” philosophy ultimately rejected historicity (e.g., causal contingency) because it assumed that, like molecules in a volume of gas, individuals change place with respect to one another so frequently that their individual positions are of no importance to the description of the greater whole. As Schopf explained in his letter to Gould, evolution happens too fast to establish preferences for particular organisms: “Sure some animals or plants are more abundant than some other animals or plants at some moment in time. But the shuffle is so fast one can’t even learn the players.” And given that assumption, Schopf revealed that his overwhelming objection to punctuated equilibria was based not on its assumption of rapid change, but rather on its assumption of stasis: “The notion of stasis—that the mean duration of a species is millions and millions of years, that then becomes the MAIN SUPPORT for a deterministic view of life!” In other words, in a world where change is extremely rare, one must conclude that it is also “special”; this implies, as Schopf put it, that “punctuated equilibrium becomes nearly the main argument for biological determinism” (Schopf to Gould, 4 December 1981: Schopf pap. 8, 31). As Schopf explained in another letter to Gould,

I hope you will see it not as a campaign against something (PE), but rather as a campaign for something (a view of the world where change is easy and continuous). I think you hit the nail-on-the-center when you said it is a question of change ‘difficult’ vs. change ‘easy’. . . . I am as convinced as I can be (&, possibly, as wrong as can be) that with $10^5$ to $10^7$ living species, & $\approx 10^{10}$ over geologic time, that species are particles in a never-ending biological world. Thus, in order to avoid Raup’s determinism . . . I am forced to a view that species durations must be quite short ($\approx 10^5$ years). If so, change must be easy. Or so it goes, in this (my) view of life (Schopf to Gould, 22 November 1982: Schopf pap. 9, 106).

7.5 Conclusion

One irony is that, while the very basis for Schopf’s view appears to be its purportedly literal reading of the fossil record, Schopf ultimately rejected that approach to reading on first principles in favor of his idealized, statistical vision. In the end, despite their initial excitement about the prospect of stochastic paleontology for producing a radically revised interpretation of the history of life, Raup and Gould each concluded that particular, historical, and deterministic factors could not be entirely abandoned. This did not mean, however, that the idealized approach to reading the fossil record was rejected as a consequence. As we will see in the next chapter, it was preserved in the approach to taxic paleobiology that negotiated many of the dichotomies—general versus particular, determinism versus randomness, selectivity versus stochasticity, models versus empirics—that lay at the heart of disagreements surrounding the MBL model. However, Schopf would not participate in this compromise. For the next several years—up until his death—Schopf clung to his species-as-particles view even as his onetime collaborators moved farther and farther away, and as a result he became increasingly bitter and isolated from his onetime compatriots. When, in 1984, Gould memorialized his friend in an obituary in the journal Schopf had founded, he acknowledged the painfulness of this fact:

Tom was a prickly, often difficult colleague, so driven by his unconventional vision, so committed to its fundamental truth, so brave (or foolhardy) that he would sacrifice friendship and human relations to its zealous advance. I can-
not psychoanalyze him. . . . But I do know one thing: I know that it led him to much personal misery. I often cried inside that he could not break out of it and spare himself the pain, but I and his other friends could do nothing. Tom was so committed to a unity of vision that he hopelessly conflated his sense of the factual with his belief about the ethical. He saw what he deeply believed as not only true but just, right, and moral. . . . But my love and admiration for him were never compromised (though I was, of course, often annoyed), for I hope we can all understand that a pure and burning commitment to knowledge and understanding drove him, often (sadly) in destructive ways (Gould 1984b, 282).

Nonetheless, Schopf's hardheaded determination to press the case for stochastic paleontology had an undeniably salutary effect on the field, and pushed paleobiology in directions that would ultimately help it to secure its place at the “high table” of evolutionary theory. Huss identifies three ways in which the MBL model innovated paleobiology, despite its “inadequacy as a theoretical model of evolution.” First, it presented a new tool—simulation—for investigating evolution that “changed paleontologic practice” by making it possible “to generate patterns from known starting assumptions (i.e., a model) and compare them with observed natural patterns.” Secondly, MBL-style computer simulations made it possible to conduct paleontological “thought experiments” that had “tremendous heuristic value.” And third, “The MBL group changed the kinds of questions paleontologists are able to ask and answer, and even the ways they are able to resolve disputes” (Huss 2009, 340). Raup somewhat more modestly concludes that while “stochastic models were developing in many fields and someone was sure to apply those methods to the fossil record,” in the end the MBL model “increase[d] awareness of the power of stochastic processes and [provided] a general warning against jumping to deterministic interpretations of pattern” (Raup, e-mail communication with John Huss, 13 March 2002).

I would add that the history of the MBL group also sheds important light on the negotiation that took place between the heterogeneous theoretical commitments of individual paleobiologists and the institutional agenda they shared. From the very start, what bound the group together was a shared commitment to creating a “nomothetic paleobiology” that would advance the status of the discipline within evolutionary biology and distance it from more traditional modes of explanation in paleontology. This commitment never faltered, despite disagreements over exactly what that nomothetic science should look like. In the end, however, Gould and Raup came to feel that a nomothetic approach could comfortably exist alongside more traditional empirical methods that emphasized historicity and even determinism, while Schopf never wavered in his belief that such factors must be rigorously excluded. This led to the demise of the MBL group, but not of the paleobiological movement itself.