Conversations about Phanerozoic global diversity

Arnold I. Miller

Abstract.—The emergence of Phanerozoic global diversity as a central theme of investigation has resulted from a confluence of factors, including the assembly by several researchers of global taxonomic databases; the advent of computers, which permitted construction and analysis of global Phanerozoic diversity trajectories; and the recognition that Phanerozoic diversity trends are important bellwethers of the evolutionary processes that cause biotic transitions. Despite the enormous progress in the measurement and interpretation of Phanerozoic diversity over the past quarter century, much of which has been reported in *Paleobiology,* these studies have collectively generated at least as many new questions as they have answered—arguably the mark of an area of inquiry that continues to be vital. In this essay, I discuss several outstanding issues in the investigation of Phanerozoic diversity, ranging from the viability of literature-derived databases for investigating global diversity trends, to the biological significance of the myriad biotic transitions that have taken place throughout the Phanerozoic.

Arnold I. Miller. Department of Geology, Post Office Box 210013, University of Cincinnati, Cincinnati, Ohio 45221-0013. E-mail: arnold.miller@uc.edu

"Do these patterns compel me to believe that bivalves and brachiopods have been locked hand to hand (or, foot to pedicle) in some sort of mortal combat for the last 500 million years? My answer is no, not really. . . ." (Sepkoski 1996: p. 242).

Introduction

In 1993, when I was co-editor of *Paleobiology,* I phoned Richard Bambach to let him know that I was accepting for publication his *Seafood through time* manuscript (Bambach 1993); that really was the title—or the first part of it. In that paper, Bambach suggested that major transitions among marine biotas through the Phanerozoic were related closely to an increase in the availability of food in the world's oceans associated with the rise of new sources of organic detritus, including land plants. He argued that many of the marine animals living on early Phanerozoic seafloors (e.g., brachiopods) required less energy than the comparatively fleshy animals that came to dominate later (e.g., clams and snails), and that the diversification of the later groups could only take place after sufficient food was available to meet their needs.

When we talked on the phone that day, Richard was curious to know what I thought of the paper. My simple response was, "I liked it."

This wasn't enough for Richard; he was not going to let me off the hook with a polite response. So, he asked, "Yes, but what did you *think* of it?"

I paused for a moment, and said, again, "I liked it." But this time, I added an additional comment: "I'd give you about a five or ten percent share of the truth."

At that point, I heard the expected snickering at the other end of the phone line. Not surprisingly, Richard thought I was sarcastically dismissing his paper. But, as I explained to him, I wasn't being dismissive at all. In my view, a five or ten percent share of the truth is actually quite good.

What I liked about Bambach's analysis was his linkage of transitions in terrestrial ecosystems to those in marine settings. It is reasonable and compelling to suggest, as several researchers now have, that changes through time in global inputs of food, nutrients, and other materials to marine ecosystems should affect the composition of marine biotas.

At the same time, despite their many virtues, I have become concerned about the large and still-growing number of studies that, like the *Seafood through time* hypothesis, suggest

overarching explanations for the history of Phanerozoic marine global biodiversity, or major subsets thereof. It is certainly understandable that researchers would seek out such explanations: the global Phanerozoic trajectory looks simple, can be described successfully with relatively few parameters (e.g., Sepkoski 1984), and can be parsed readily into groups of one's choosing that exhibit diversity zeniths during different portions of the Phanerozoic, with one group giving way sequentially to the next. However, there is an expanding body of evidence suggesting that a good deal of complexity resides beneath the global veneer: at local and regional levels, biodiversity transitions tend to be highly episodic (cf. Ivany and Schopf 1996) and, during at least some extended intervals, there is, at best, only limited global synchronicity to these episodes (Miller 1997a).

During the past several years, I have gravitated to the view that the global Phanerozoic diversity trajectory is the product of a spectrum of mechanisms that operate at multiple scales (Miller 1998). On the one hand, this might seem so blatantly obvious as to be trivial. And yet, the alternative view, that global patterns have been mediated mainly by global-scale processes—be they biotic interactions among biotas played out over geological time (e.g., Thayer 1979; Sepkoski 1984) or, at the other end of the spectrum, the direct consequences of mass extinctions (Gould 1985)—has certainly figured prominently in the literature.

This viewpoint might seem like a surrender to the complexities of a world that is dynamic physically and biologically at a variety of spatio-temporal scales. In fact, it is nothing of the kind. Because of our rapidly improving understanding of local and regional biotic patterns and their relationships—or not—to physical attributes of the settings in which they lived, there is good reason to be optimistic about our chances of one day understanding the intricacies of local and regional patterns, and how they weave together to produce the global signals with which we are all familiar.

Despite the enormous progress of the past quarter century, or maybe because of it, nearly every facet of the study of Phanerozoic diversity trends remains contentious, and I cannot pretend to suggest definitive research programs to solve the most pressing issues. What I can hope to do, however, is to frame some of these issues in a way that might make them more accessible to the broad audience interested in global diversity. As a vehicle for doing so, my discussion below will be woven with descriptions or excerpts of various conversations that I have engaged in over the years with friends and colleagues. Snippets from these conversations are worth recounting because they have helped me to (1) crystallize my viewpoints, (2) set a personal research agenda, and (3) recognize my own foolishness at times. Maybe they can help some readers to do the same.

I will focus below on a set of intertwined issues related to the taxonomic diversity of Phanerozoic marine biotas. These include the assembly and use of taxonomic databases, the calibration of Phanerozoic diversity trajectories, the causes of major global transitions in biotic composition, the extent to which Phanerozoic diversity trends transcend geographic and ecological scale, and the extent to which biotic transitions have been mediated by physical transitions and perturbations.

There are several additional themes that I will not pursue in this presentation despite their obvious relevance to Phanerozoic diversification, including the relationship between taxonomic and morphologic diversity (e.g., Foote 1993; Wagner 1995); similarities and differences in factors that affect diversity in marine and terrestrial settings (e.g., Valentine et al. 1991; Eble 1999); and the correlation—or not—between transitions in taxonomic diversity and relative abundance (e.g., McKinney et al. 1998; Lupia et al. 1999). While these and other themes will clearly be of significance to the eventual understanding of biotic transitions, my aim here is to discuss issues that must be settled before we can get our taxonomic diversity house in order.

Eavesdropping on an Internet Conversation, July, 1999: Counting Taxa

Okay, this first one wasn't *my* conversation. Rather, it was a portion of an Internet conver-

sation that took place during July, 1999, on the *PaleoNet Listserver*, an online discussion forum for paleontologists. But first, a bit of perspective:

Over the years, perhaps more than any other endeavor in the field of paleontology, the study of global biodiversity has been emblematic of the changes that the discipline has undergone. Paleontology has been transformed from a science that was once largely descriptive to a more synthetic enterprise in which information about fossils is assembled into databases, and the data are then analyzed to address large-scale questions that could not possibly have been evaluated exhaustively by our pre-1950 forbears, because of the lack of computers (but see below). This transition is hardly unique to our field and, undoubtedly, many other sciences have experienced the kind of resultant squabbling that has popped up intermittently on the pages of paleontological journals and at scientific meetings. Still, one would think that, by now, the primary issues had long been settled concerning the assembly of published information about fossils into databases, the tabulation of these data to produce global diversity curves, and the use of assembled databases to test hypotheses about the history of diversity. But the squabble goes on. With that as a backdrop, here are some excerpts from one participant in the *PaleoNet* discussion (references to taxa, periods, and dates have been deleted to protect the identity of the *PaleoNet* correspondent):

Bluntly: . . . non-systematists, people with no detailed knowledge of the group at hand, shouldn't bother compiling taxonomic databases. The taxonomic literature is byzantine, wildly variable in quality, approach, basic philosophy, etc., etc. Databasing it requires subjective taxonomic decisions to be made at every turn. Even a very thorough trawl of the primary literature (as opposed to the usual Treatise / Zoo Rec productions) may generate little more than noise without the application of specialist knowledge. Ok, I better qualify that 1) I have direct experience only of [taxon deleted]; but for [taxon deleted], I can affirm that the situation is absolutely, positively that

bad—in many groups, the white noise of bad, weird, lunatic fringe taxonomy generates distortion of over 100% in terms of raw counts, and [period and taxon deleted] taxa still have basically no philosophical / methodological connection to post-[period deleted] taxa. 2) The [taxon deleted] Treatise still mainly dates to [date deleted]. . . .the Treatise in general is very much a Good Thing, and may be an excellent source of standardized data for many animal groups for which recent revisions are available.

Anyway, the point of the preceding rant is that "meaningful" taxonomic data aren't objective entities that anyone can gather up, and require an investment of more than just time. Sure, you can just go and gather s(tuff) up, and people obviously have.

These comments suggest that data collected by "non-specialists" not only are bound to be deeply flawed, but may well produce distorted patterns that cannot be trusted. (I will not bother to address the suggestion that "non-systematists" who assemble synoptic, biodiversity databases typically do so blindly, and mainly by mining data directly from the *Treatise* or the *Zoological Record*, except to note that the days when database assemblers *limited* their compilations to those kinds of sources, rather than the primary literature, ended more than 20 years ago.)

Several papers in recent years have analyzed directly the significance of possible shortcomings in paleontological data, focusing on the question of taxonomic validity of the taxa under investigation, as well as the extent to which improvements and additions to available data over a period of time change perceptions about paleontological patterns. These include Sepkoski's (1993) recognition that accumulated changes to his global compendium of fossil marine families over ten years yielded remarkably little change to the Phanerozoic trajectory of global marine diversity; Maxwell and Benton's (1990) demonstration that 87 yr of improvement to the data available on tetrapod families did little to alter the major features of the diversity trajectory of Phanerozoic tetrapod families; Sepkoski and Kendrick's (1993) finding that paraphyly is

probably not a significant problem in the analysis of biodiversity patterns at the genus and family levels; Benton's (1995) publication of an aggregate diversity trajectory for marine families for the Phanerozoic that closely paralleled Sepkoski's earlier depictions, despite the use of a different database; and Foote's (1997) demonstration that, for several higher taxa, the addition of data from future fossil discoveries is unlikely to change the already-emergent picture of their overall morphological variability and disparity. More recently, Benton (1999) offered a thoughtful rejoinder to those who continue to suggest that paleontological databases are not up to the tasks for which they have been utilized, and I encourage interested readers to consult his paper.

Still, the comments of the *PaleoNet* correspondent point to the need for further, *direct* evaluation of the concern that data not properly vetted or otherwise updated by specialists may yield—or perhaps has already yielded—untrustworthy signals. In the "ideal" analysis, global-scale diversity patterns extracted from databases compiled by nonspecialists would be compared with those based on compendia for the same higher taxa produced and vetted by specialists. Just such an analysis was conducted for trilobites in a recent paper by Adrain and Westrop (2000), who compared lower Tremadocian through upper Wenlockian genus diversification patterns based on Sepkoski's unpublished compendium to those generated from their own state-of-the-art database. Adrain and Westrop's database, which has permitted an extensive investigation of trilobite macroevolution throughout the early Paleozoic (e.g., Adrain et al. 1998, 2000; Westrop and Adrain 1998), was compiled largely from direct, critical evaluation and vetting of previous systematic research on trilobites, as well as from extensive field and laboratory investigations. In comparison to their database, Adrain and Westrop (2000) demonstrated that Sepkoski's compendium contained a large number of systematic and stratigraphic errors. Nevertheless, the global diversity trajectory extracted from Sepkoski's compendium was nearly identical to that developed with their database (Adrain and Westrop 2000: Fig 3). Thus, the authors
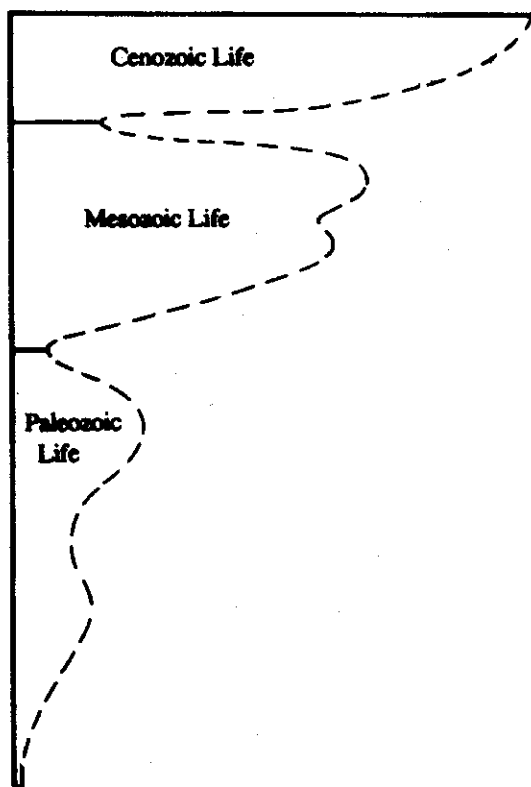

FIGURE 1.   Phillips's depiction of the changing number of marine species through geological time, based on a compendium of fossil data from Great Britain (redrawn from Phillips 1860: Fig. I).

concluded that Sepkoski's compendium produced an accurate depiction of the large-scale, global diversity trajectory.

Adrain et al. (1998, 2000; Westrop and Adrain 1998) produced significant conceptual advances in perceptions about the macroevolutionary history of trilobites that clearly could not have been achieved through reliance on Sepkoski's compendium. However, these advances resulted not so much from taxonomic revision to global compendia as they did from the thoughtful, and novel, ways in which these workers have analyzed their data and extended their databases to include geographic regions neglected in previous compilations. Just as importantly, they have moved beyond the relatively coarse global scale to rigorously address paleogeographic and paleoenvironmental aspects of diversification, both of which should now be viewed as prerequisites

for the interpretation of global diversity patterns (see below).

While I have no doubt that concerns about taxonomic problems are well justified at relatively fine scales, and certainly call for continued taxonomic analyses and improvements to fossil databases, I doubt strongly that further improvements to the *taxonomic quality* of paleontological databases will affect how we perceive large-scale biodiversity patterns, at least among marine biotas. This is not to claim that the interpretation of global diversity trajectories is uncontroversial. But it is time to acknowledge, once and for all, that, from a taxonomic standpoint, the data already at hand are of sufficient quality—and have been for quite some time—to provide a faithful rendition of large-scale, global diversity trends as preserved in the marine fossil record. There are two primary reasons that this is the case. First, most of the major features of global diversity curves, including global radiations and mass extinctions, are not subtle and would not turn on the misassignment of even a moderate number of taxa. Second, many of the trends delineated in global diversity trajectories have been recognized through protracted intervals of geological time, and if bad taxonomy did produce them, it would have taken something approaching a series of nonrandom conspiracies of bad taxonomy, sometimes among workers focusing on diverse sets of higher taxa. If anything, taxonomic problems should obscure, rather than produce, the patterns observed (Benton 1999).

Washington Island, Wisconsin, August, 1996: Forging a Consensus

In recent years, it has become fashionable to cite the groundbreaking work of Phillips (1860) as the source of the first Phanerozoic diversity curve; clearly, Phillips deserves credit for this and more. His depiction of Phanerozoic species diversity (Fig. 1), which was based on a comprehensive compilation of fossils described from British strata (Morris 1854), involved more than simply tabulating the total number of species present within each of several stratigraphic intervals through the Phanerozoic. Because there were drastic differences in stratigraphic thickness (and vol-

Z. *Zoophyta*
Cr. *Crustacea*
B. *Brachiopoda*
E. *Echinodermata*
M. *Monomyaria*
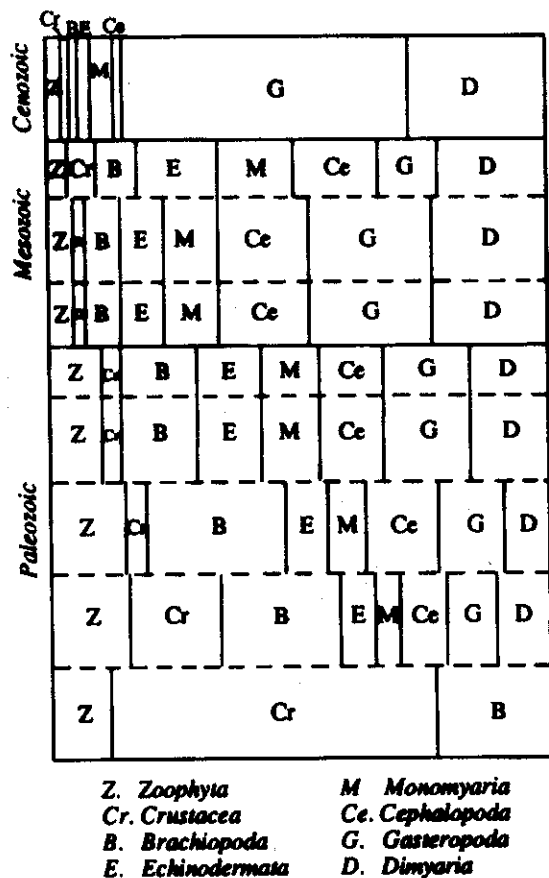Ce. *Cephalopoda*
G. *Gasteropoda*
D. *Dimyaria*

FIGURE 2. Phillips's depiction of the changing composition of marine invertebrate biotas through the Phanerozoic (redrawn from Phillips 1860: Fig. 6; taxonomic designations, some of which are outdated, are from Phillips).

ume) from interval to interval and, all else being equal, a thicker interval might be expected to contain more species simply because of its greater volume, Phillips sought to overcome variation in interval thickness by recalibrating diversity values for each stratigraphic interval as the number of species per unit thickness (1000 feet) (see Phillips 1860: Fig. 3 for an example from the Ordovician and Silurian). The resulting curve mitigated the overwhelming dominance of Paleozoic strata relative to younger rocks in Great Britain and suggested that, per unit thickness, Cenozoic strata were far more species-rich than those of the Paleozoic. Without Phillips's volumetric correction, species diversity on the curve would have peaked sometime during the Paleozoic.

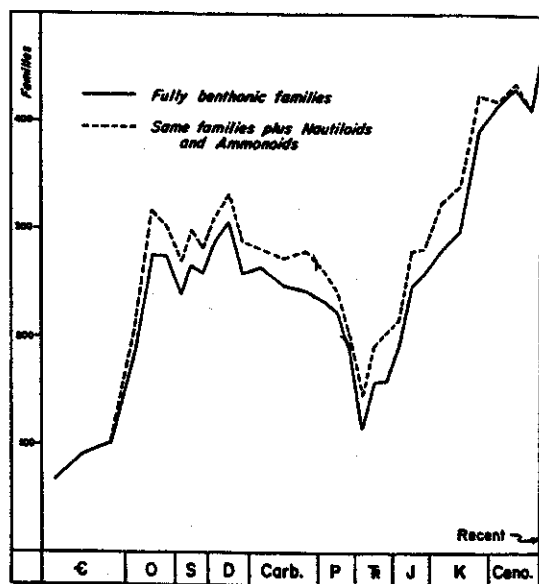For any number of reasons, Phillips's curve

FIGURE 3. Valentine's depiction of the diversity of Phanerozoic marine families, compiled from an aggregate database for nine well-skeletonized marine phyla (reprinted from Valentine 1969: Fig. 5; published by permission of the Palaeontological Association).

FIGURE 4. Valentine's estimated trajectory of Phanerozoic species diversity (reprinted from Valentine 1970: Fig. 2).

might not accurately depict Phanerozoic trends in global marine biodiversity. For one thing, the database on which it is based was confined to Great Britain. Moreover, no diversity values are actually recorded on the graph, although these numbers would only be of limited use in any absolute sense, given the correction for thickness. In addition, it is not clear how many separate Phanerozoic stratigraphic intervals (data points) were evaluated to produce the curve. Nevertheless, the general trends that Phillips depicted are strikingly similar to those recognized in more recent compilations that were global in scope, as are the transitions among major faunal elements that he also illustrated (Fig. 2).

The strength of this signal became apparent during the '60s and '70s, when several researchers recognized similar patterns using data collected at various taxonomic levels with disparate methodologies (see Newell 1967 and other references cited below). However, a major debate ensued about the biological veracity of the signal, starting with Valentine's (1969, 1970) compilations of Phanerozoic global diversity from an aggregate database for nine well-skeletonized marine phyla. Valentine
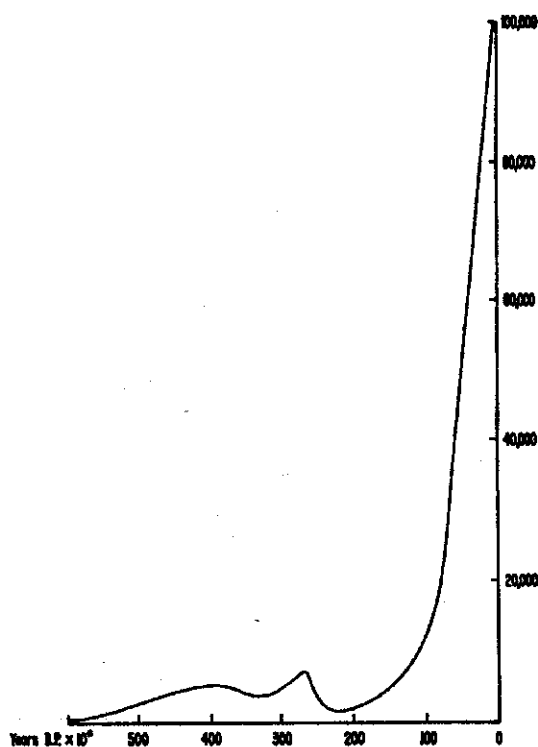
presented diversity curves at taxonomic levels ranging from phylum to species (e.g., Figs. 3, 4), based on data contained mainly in three sources published in the 1950s and 1960s: the *Treatise on Invertebrate Paleontology, Osnovy Paleontologii,* and *The Fossil Record.* Whereas the curves for higher taxonomic levels were compiled directly from these data, these literature sources did not contain species-level data. Thus, Valentine's species-level curve was an approximation, based primarily on an estimate of the total number of present-day species yielded by the nine phyla in question; inferences about the ratios of the number of taxa expected—all else being equal—from one taxonomic level to the next; and changes in inferred levels of faunal provinciality.

Among the Phanerozoic diversification patterns that Valentine documented with his compilations were the striking differences in trajectories exhibited at different taxonomic levels and a dramatic post-Paleozoic increase at the family level and lower. He explained

these patterns in the context of ecological and geological transitions that characterized the history of life and the physical history of the earth, suggesting that diversification at higher taxonomic levels characterized the initial, early Paleozoic radiation, whereas post-Paleozoic diversification took place mainly at lower taxonomic levels as a consequence of increasing provinciality. These differences in taxonomic attributes of diversification were confirmed subsequently by Erwin et al. (1987), who compared diversification in the wake of the Late Permian mass extinction to that during the early Paleozoic radiations.

Valentine's species-level curve (Fig. 4) is particularly striking, in that it suggests a Cenozoic increase in standing diversity of approximately one order of magnitude. Moreover, Valentine clearly considered the patterns on his curves to be *real*, in the sense that he did not view them as consequences of artifacts that would compromise their biological significance.

Shortly thereafter, however, a different view was presented by Raup (1972), who showed that that there were strong similarities between diversity trajectories compiled for Phanerozoic families and genera and those depicting the changing availability of sedimentary rock through geological time. Recognizing that the quality and quantity of fossil sampling probably improved through the Phanerozoic, Raup further showed with computer simulation that differences between apparent trajectories produced at various taxonomic levels could have been direct consequences of a secular improvement in sampling (see Raup 1972: Fig. 5).

In a pair of subsequent papers, Raup (1976a,b) presented his own compilation of Phanerozoic marine species diversity with a database generated by sampling the *Zoological Record* for citations to new fossil species belonging to 19 higher taxonomic groupings. The resulting diversity trajectory exhibited a two- to threefold increase in Cenozoic diversity, which was far more modest than Valentine's estimate. Following on his earlier paper, Raup demonstrated correlations between Phanerozoic species diversity and sedimentary rock volume/area (see Fig. 5). While
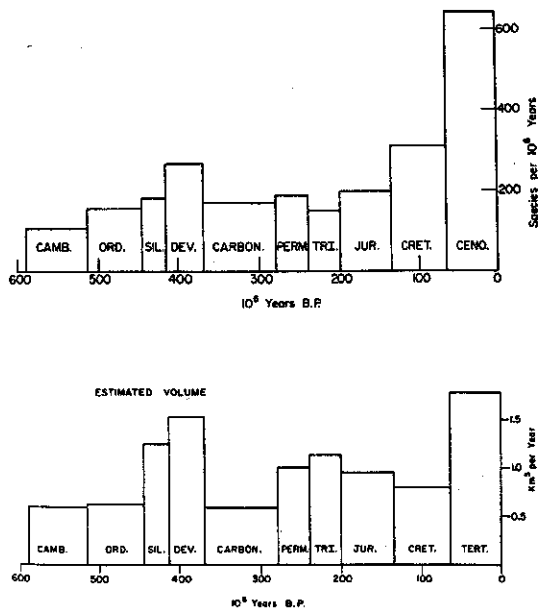

FIGURE 5. A comparison from Raup of apparent species diversity through the Phanerozoic (upper graph) versus the estimated volume of sedimentary rock for the corresponding stratigraphic intervals (lower graph). (Upper graph is reprinted from Raup 1976a: Fig. 2; lower graph is from Raup 1976b: Fig. 2.)

Raup was careful not to rule out the possibility of a biologically meaningful post-Paleozoic diversity increase, he noted that "there is no compelling evidence for a general increase in the number of invertebrate species from Paleozoic to Recent."

Against the backdrop of the ambiguities suggested by Raup, Bambach (1977) presented a new approach intended to overcome the problem of sedimentary rock volume. Bambach determined the species richness for each of 386 fossil communities delineated mainly in North America and England/Wales, and then calculated, for several Phanerozoic intervals, the *median* species richness of communities contained within each of three designated "habitat types." Recognizing that the number of lists would likely be influenced by the amount of the sedimentary rock within the intervals available for sampling, Bambach used medians, and thus his richness values were not dependent directly on the number of faunal lists contained within each stratigraphic interval. Interestingly, Bambach's period-to-period median-richness trajectory exhibited

by the values from "open marine environments" closely paralleled that observed in Raup's (1976a) compilation of species diversity, suggesting that there is a robust, broad Phanerozoic diversification trajectory that can be recognized regardless of whether (1) there is a "correction" for secular changes in rock volume; (2) relative richness is based on within-community values or on sampling of the aggregate, global record; or (3) the geographical purview of the analysis is limited to a fair extent.

This theme of comparability among different databases was expanded and addressed explicitly in a landmark study published by Sepkoski, Bambach, Raup, and Valentine (1981). Period-by-period Phanerozoic diversity trajectories were juxtaposed for five different databases (Fig. 6): Bambach's (1977) median species richness for open marine environments; Raup's (1976a) global species diversity; median ichnospecies richness in neritic and flysch facies based on data provided in sources published by Seilacher (e.g., Seilacher 1974); global genus diversity based on a transformation to the data provided by Raup (1978); and global family diversity based on data from Sepkoski (see Sepkoski 1982). The remarkable similarities exhibited by the five trajectories motivated the authors to conclude first that there is a strong, underlying trajectory to Phanerozoic diversity that transcends the varying idiosyncrasies of the five data bases, and second that this trajectory is biologically meaningful, and not a consequence of preservational or other artifacts.

That this paper is known commonly by two different nicknames (the "consensus paper" and the "kiss and make up paper") is strong testimony to its influence on the field. After a decade of disagreement about the meaning of the emerging Phanerozoic diversity signal, two main protagonists in the debate, Raup and Valentine, signed on to a paper that reached conclusions at odds with positions that they championed earlier. For Valentine, the concession was relatively mild: by accepting Raup's species-level trajectory, he was conceding tacitly that there had not been an order-of-magnitude diversity increase in the Cenozoic. Raup's concession was arguably far
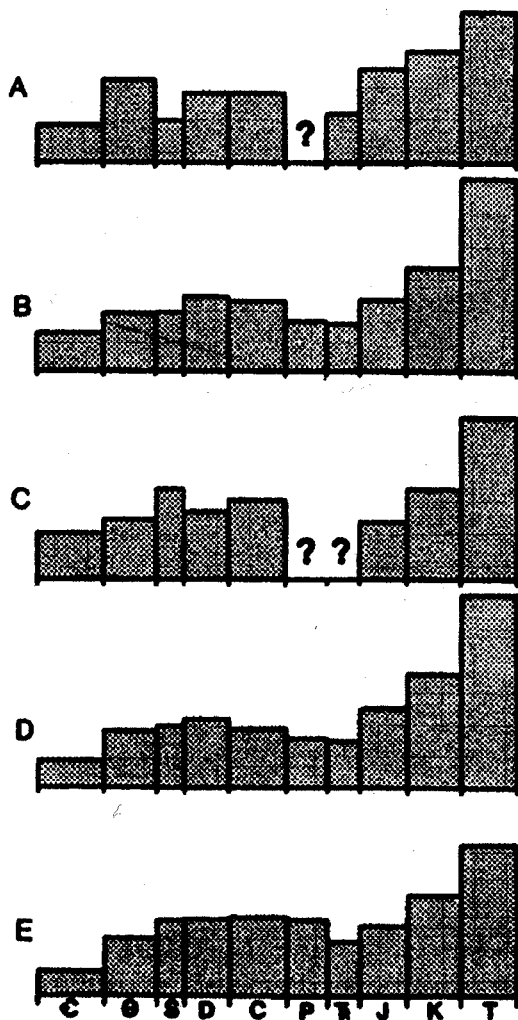

FIGURE 6. A comparison of five different compilations of taxonomic diversity through the Phanerozoic. A, Median richness of ichnospecies assemblages, using data acquired from Seilacher (1974 and other papers). B, A slightly modified version of Raup's (1976a) depiction of species diversity. C, Median species richness of communities in "open marine environments," from Bambach 1977. D, Genus diversity, using data from Raup 1978. E, Family Diversity, using data from Sepkoski. (Reprinted from Sepkoski et al. 1981: Fig. 1, by permission from Nature copyright 1981 Macmillan Magazines Ltd.)

more significant, and its effects reverberate even today: he abandoned his position that the post-Paleozoic increase might be an artifact. Sepkoski's (1981) much more highly resolved global Phanerozoic diversity trajectory (Fig. 7), in which marine families were parsed with factor analysis into the three "evolutionary faunas," was published shortly before the con-
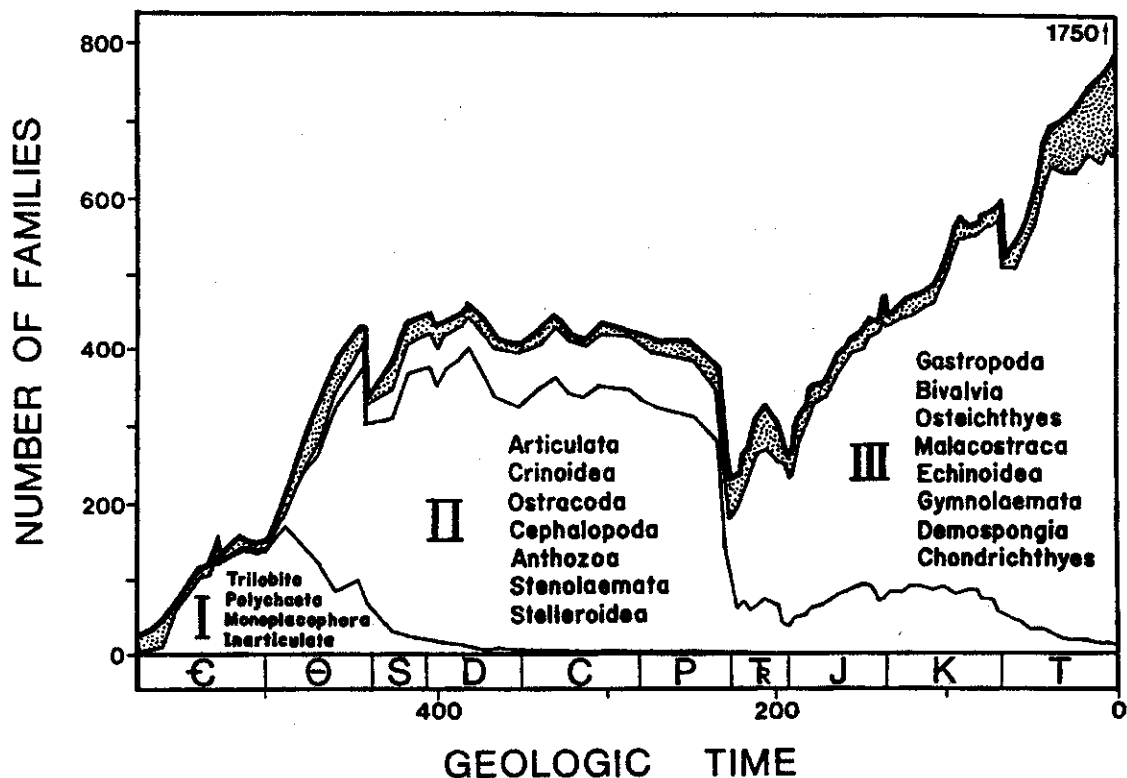
FIGURE 7. Depiction of the diversity of Phanerozoic marine families, with the three "evolutionary faunas" delineated, based on a factor analysis of a global compendium of fossil marine families. On the graph, the evolutionary faunas are depicted with roman numerals: I, Cambrian Fauna; II, Paleozoic Fauna; III, Modern Fauna. Subsequent analyses of updated databases (e.g., Sepkoski 1993) did not appreciably alter the patterns depicted in this figure. (Reprinted from Sepkoski 1981: Fig. 5.)

sensus paper, and subsequently became a kind of "industry standard," the major features of which numerous researchers have sought to explain in biological contexts. However, it can be said with some justification that this status could not have been achieved without the cover provided by the consensus paper.

To me, Raup's turnaround had always been rather puzzling: what had motivated him to change his mind? In 1997, I had an opportunity to ask him about this directly, during a visit to his home on Washington Island, Wisconsin. Given that more than a decade and a half had transpired since publication of the consensus paper, his recollection about his decision to join the paper was a bit hazy. Nevertheless, he remembered that he had been unhappy about his disagreement during the 1970s with Valentine over the magnitude of the species-level diversity increase, and he

saw the consensus paper as a kind of numerical splitting of the difference between two rather disparate views:

I was so delighted to see support for the view that a lot of the increase that Jim Valentine had observed couldn't be substantiated—it was a numerical compromise.... [A]s I read this second '76 paper [Raup 1976b]—"there is no compelling evidence for the existence of a trend"—that doesn't say that there *isn't* a trend and, to me, this consensus paper was supportive in that it reduced the increase to something almost down in the noise level of the sample. It was clearly a step in my direction.... Also, Jim Valentine had... plotted and published the factor of ten [graph]—his certainly represented the very strong conventional wisdom that everybody had—and so the consensus paper—I saw as a se-

vere break with the conventional wisdom—not only Jim Valentine, but everybody else. . . .[A]lthough I happily agreed to be an author on the consensus paper, I don't remember agreeing with it. But it was a lot closer to my position than I thought possible.. . . [A]n important element of this is that at no point did I think I had a case for level or declining diversity. The only thing I had a case for was the *possibility* of level or declining diversity. Therefore, I didn't have an advocacy position to lose.

Nevertheless, it became clear later in our conversation that, even if his earlier work had not *proven* that Phanerozoic diversity had achieved and maintained a fairly steady level through most of the Phanerozoic, Raup continues to believe that the effects of potential sampling artifacts on the Phanerozoic diversity trajectory have not been tested adequately, and we spent much of our remaining conversation discussing how one might conduct such tests. In fact, he went so far as to note humorously, in reference to his 1976 papers: "And, damn it, this rock volume curve looks so much like these [diversity curves]."

Therefore, while most readers would perceive the consensus paper as a strong statement about the biological reality of a threefold late Mesozoic and Cenozoic increase in diversity at the family level and below, it is clear that at least one author of the consensus paper continues to harbor doubts. But, given the results highlighted in the consensus paper, why should doubts remain? Two primary reasons come quickly to mind: First, of the five graphs depicted in the consensus paper, three (Raup's curves at the genus and species levels, and Sepkoski's at the family level) are subject directly to the rock volume problem. Second, while the remaining two graphs (based on Bambach's within-habitat median species-richness values and Seilacher's trace-fossil data) should not be similarly affected by changing rock volumes, this does not mean that they are free of sampling concerns. For example, the major Cenozoic increase in Bambach's North-America-dominated data could reflect the transition from lithified to unconsolidated sediments in the North American

stratigraphic record, as exemplified in the Cenozoic record of the coastal plain. Well-preserved fossils are much more easily extracted from unconsolidated sediments, which would tend to inflate the taxonomic richness of a Cenozoic sample relative to one collected from an older, lithified stratum. In addition, there is no reason to expect a priori that within-habitat (alpha) diversity trajectories, like those based on Bambach's and Seilacher's data, should correlate directly with synoptic, global-scale trajectories (see below).

Rather than relying on sedimentary rock quantity as an indirect proxy of sample size, a more effective approach is to assess *directly* from fossil data whether the Phanerozoic trajectory is affected by variations in sampling intensity from interval to interval. This approach requires the development of databases that record the occurrences of taxa in multiple locations/strata for each sampling interval; the frequency of occurrence of a particular genus in a given database thus reflects the relative frequency of its occurrence in strata from the interval under study. These data can then be "sampling standardized" using rarefaction and other techniques that permit a researcher to ask whether the genus richness of a larger sample from one time interval exhibits an inflated taxonomic richness relative to an interval with a smaller overall sample simply because of the difference in sample size. This approach has been used by Miller and Foote (1996) to assess the series-to-series diversity trajectory of global marine genera during the Ordovician Radiation, and by Alroy (1996, 1998) to correct the genus- and lineage-level diversity trajectories of Cenozoic mammals in North America. In both instances, sampling-standardization produced notable changes to the raw, uncorrected diversity trajectories. The task of "correcting" the entire Phanerozoic marine trajectory seems daunting indeed, but just such an effort is now underway under the auspices of a working group anchored at the National Center for Ecological Analysis and Synthesis. One goal of this group project, entitled "A sampling-standardized analysis of Phanerozoic marine diversification and extinction," is to construct a database of Phanerozoic genus occurrences that will permit the

application of sampling-standardization techniques to extensive Phanerozoic intervals. To date, the majority of effort has focused on the acquisition of data for two major intervals, including one in the Paleozoic (Middle Ordovician through Lower Carboniferous) and another straddling the Mesozoic/Cenozoic boundary (Upper Jurassic through Eocene). Preliminary results (J. Alroy et al. unpublished) suggest that published raw diversity trajectories may exaggerate the increase in diversity during the late Mesozoic–Cenozoic.

Telephone Conversation, Warwick to Cincinnati, August, 1998: Is Global Diversity Mediated by Global-Scale Processes?

The empirical pattern of marine diversity presented by Sepkoski (1981) provided immediate impetus for the investigation of several intertwined issues. In a sequence of papers, Sepkoski (1978, 1979, 1984) argued that the major features of Phanerozoic diversity could be modeled successfully and meaningfully with logistic equations. In doing so, he contended that global taxonomic diversity could be treated in much the same way that MacArthur and Wilson (1963, 1967) treated the colonization of an island over ecological time, but scaled-up spatially and temporally to model the changing taxonomic richness of the earth over geological time. However, Sepkoski focused on two features of Phanerozoic diversity that argued for something more than simple logistic growth and stabilization in taxonomic diversity: (1) the apparent failure of diversity, measured at the family level, to achieve and maintain a steady state; (2) the transition in global biotic composition from clades with high turnover rates that characterized the Cambrian and Paleozoic Evolutionary Faunas, to others with lower turnover rates representative of the Modern Evolutionary Fauna (Sepkoski 1981). To incorporate these features, Sepkoski (1984) developed three coupled (i.e., interactive) logistic equations (or "phases") that accommodated the apparent behavior in raw, global diversity trajectories of the three evolutionary faunas. The system was driven by differences in the initial rates of diversification of each of the three
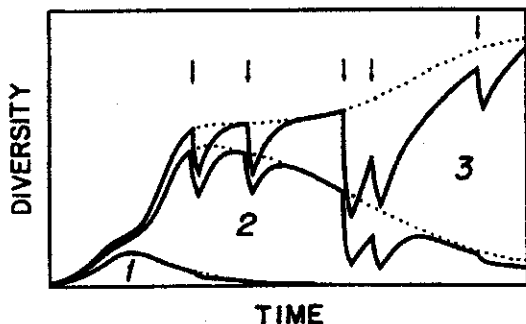

FIGURE 8. A three-phase, coupled logistic model of Phanerozoic familial diversification, with the five major Phanerozoic mass extinctions incorporated. The dotted lines illustrate the trajectories that each of the three modeled evolutionary faunas followed when mass extinctions were not included. (Reprinted from Sepkoski 1984: Fig. 8C.)

modeled evolutionary faunas, as well as by differences in the rates at which their respective origination and extinction rates converged as diversity increased. The fit of the three-phase model to the actual Phanerozoic family diversity trajectory was quite impressive, especially when mass extinctions were incorporated (Fig. 8).

In Sepkoski's view, the coupled logistic model provided more than just a means to summarize Phanerozoic global marine diversity. The success of the model motivated two fundamental suggestions about the processes responsible for the observed patterns: first, that the history of biodiversity was mediated by global-scale interactions among higher taxa or groups of higher taxa (evolutionary faunas in this case) over geological time (see also Kitchell and Carr 1985), and second, that mass extinctions only perturbed the pattern temporarily, but did not alter it permanently. To these, a third implication can be added: that the biotic transitions observed in synoptic, global diversity curves have been driven by global-scale dynamics.

Sepkoski was not the only researcher to view the history of Phanerozoic diversity in the context of equilibrium dynamics. However, his vision of multiple equilibria, with biotic transitions driven by global-scale interactions, was a unique application of the equilibrium concept, with its own implications for the history of global biodiversity. By contrast, Rosenzweig (1995 and elsewhere) echoed Raup's

(1976b) suggestions that Phanerozoic diversity has been at equilibrium since the Paleozoic—except temporarily during mass extinctions—and, failing that, that global diversity increased because of the colonization of new habitats or the realization of previously unexplored niches (cf. Bambach 1985). Courtillot and Gaudemer (1996) provided yet another view, arguing that Phanerozoic could be modeled with a sequence of four simple logistic functions, the parameters of which were altered and reset by mass extinctions. Thus, they envisioned a central role for mass extinctions in mediating the history of biodiversity.

Regardless of which, if any, of these alternatives more closely describes what transpired in the history of global diversity, they all suggest some level of de facto global mediation associated with the presumably finite amount of ecospace available throughout the world. This assessment appears to be supported by a host of studies suggesting that taxonomic origination rates and probabilities declined through time, both within higher taxa (e.g., Gilinsky and Bambach 1987; Alroy 1998; Eble 1999) and in the global biota tracked through the Phanerozoic (e.g., Gilinsky 1998), an expectation of a system that is filling up with taxa. Because secular declines in origination rates within higher taxa would not be expected in a system where diversification occurs without limitation, these observations also appear to obviate Benton's (1995) claim that Phanerozoic diversity in marine and terrestrial settings has not approached equilibrium and has exhibited a long-term exponential increase. Benton has since modified this claim, at least for marine organisms (Benton 1997).

Recently, I suggested an alternative to Sepkoski's vision of a central role for biotic interactions in causing the long-term Phanerozoic transitions among constituents of evolutionary faunas (Miller 1998), observing that (1) the Phanerozoic-scale transition from taxa with higher turnover rates to others with lower rates, which can be explained with the coupled logistic model, could instead have been caused by physical perturbations at myriad scales that "weeded out" the more volatile higher turnover taxa (see Gilinsky 1994 and others); and (2) when dissected into their local and regional components, diversity trends that appear gradual at the synoptic, global scale, appear, instead, to be highly episodic and typically linked to physical perturbations. Carrying these observations to the extreme, I argued that biotic transitions throughout the Phanerozoic might have been mediated not by global-scale interactions, but rather by physical perturbations ranging in scale from the global events that induced mass extinctions to the local events that induced regional biotic turnover within a single depositional basin (e.g., Patzkowsky and Holland 1993, 1999; Brett and Baird 1995).

Shortly after I published this view, Jack Sepkoski called me from his home in Rhode Island to talk about my paper and our apparent disagreement. While he noted that he was comfortable with the prospect raised in several of my earlier papers of a possible link between diversification and tectonic activity during the Ordovician Radiation (e.g., Miller and Mao 1995), he pointed out that changes through the entire Phanerozoic in levels of tectonic activity or in any other physical aspect of the earth were unlikely to be reflected in the biodiversity changes that we observe through the Phanerozoic. Further, he suggested that my observations about the apparent breakdown of global-scale patterns at the local level could be viewed mainly as reflecting simple patchiness at a relatively fine paleogeographic and paleoenvironmental scale of a pattern that is nevertheless apparent and governed by a broader dynamic at the global scale.

In considering this issue of scale, it is worth drawing an analogy to biotic patterns that we expect on a seafloor along a sampling transect that traverses an environmental gradient; in this analogy, the environmental gradient as a whole corresponds to the global biota, and individual locations along the gradient correspond to the biota within limited, constituent geographic regimes. Although Whittaker (1975) once likened environmental gradients to continuous spectra, the reality is that no environmental gradient is infinitely continuous. If we sample any environmental gradient with sufficiently fine lateral spacing across its entire extent, we should discover, instead, that

every gradient contains some number of zones, or "steps," within which we would expect samples to vary randomly because of local patchiness, rather than in continuous lock-step with the gradient (Miller and Cummins 1990). Of course, the discovery of patchy distributions at fine lateral scales within these zones would not negate the reality of the gradient at a broader scale.

The validity of this analogy with respect to Phanerozoic global diversity hinges on the relationship between the finer-scale patches and the broader-scale pattern. In the case of the diagnosis of an environmental gradient on a seafloor, it would not be worthwhile or particularly informative to map all of the patches within a single step, because there is no reason to expect that variation on the scale of the patches *causes* the broader patterns that we observe along the gradient. By contrast, in the case of Phanerozoic diversity (1) we can do an effective job of mapping out the relevant "patches" in space and time; i.e., the regional units of relative faunal uniformity—if not co-ordinated stasis—that are bounded by intervals in which the rate of biotic change is accelerated (see Patzkowsky and Holland 1997 for an example); and (2) it is possible to test whether episodic, physically induced transitions at scales that range from global to regional combine to produce, and therefore "cause," global patterns. This issue is further considered below.

On a Train, Somewhere between Valencia and Barcelona, Spain, October, 1999: Avoiding Straw Men in the Search for Physically Mediated Scale-Independence

In a series of papers, Aronson (e.g., 1994; Aronson and Plotnick 1998) has established *scale-independence* as a valuable unifying concept with respect to biotic transitions: processes that govern and explain patterns observed on relatively fine spatio-temporal scales may also scale up to explain large-scale biotic transitions that are observed in geological time. There are numerous examples of this concept, some of which involve interactions among clades and others involving interactions among ecological groups that may have diverse taxonomic memberships. Martin

(1998) has extended the concept further by suggesting that nutrient-related phenomena affecting biotic patterns on limited spatio-temporal scales might also explain global biotic transitions associated with Phanerozoic-scale changes in energy availability (e.g., Bambach 1993; Vermeij 1995).

(I will not discuss here the emerging body of literature suggesting that biodiversity patterns exhibit a hierarchical structure that is self-similar and that their behavior through time can be explained by models that incorporate self-organized criticality [see Solé et al. 1999 for a concise review]. For the moment, I am not sure how to interpret the admittedly seductive results emerging from this body of work, given that they require a degree of global connectedness among species that remains unsupported. However, I recognize that this research is still in its infancy, and I look forward over the coming years to the continued development and discussion of this perspective.)

Benton (1987, 1991, 1996) summarized a spectrum of possible relationships between the global diversity histories of two clades through geological time in cases where one clade declines to extinction and the second undergoes diversification. These relationships ranged from a pattern of waning in one clade matched by waxing in another (the "double wedge" of some authors), to a total lack of an apparent relationship between the two clades in which their respective histories were mediated by differential responses to a mass extinction episode (Fig. 9).

As recounted by Gould and Calloway (1980) the notion has been around at least since Darwin that the demise of one taxon might be caused by the rise of another. Among marine and nonmarine tetrapod families that he investigated, however, Benton (1996) showed that instances in which one family replaced another because of competition are probably quite uncommon, when information on geographic, ecological, and temporal overlap were considered. Typically, suggestions of competitive replacements among higher taxa are based on the contention that a group exhibiting a diversity increase was, in some way, competitively superior to a group exhibiting a
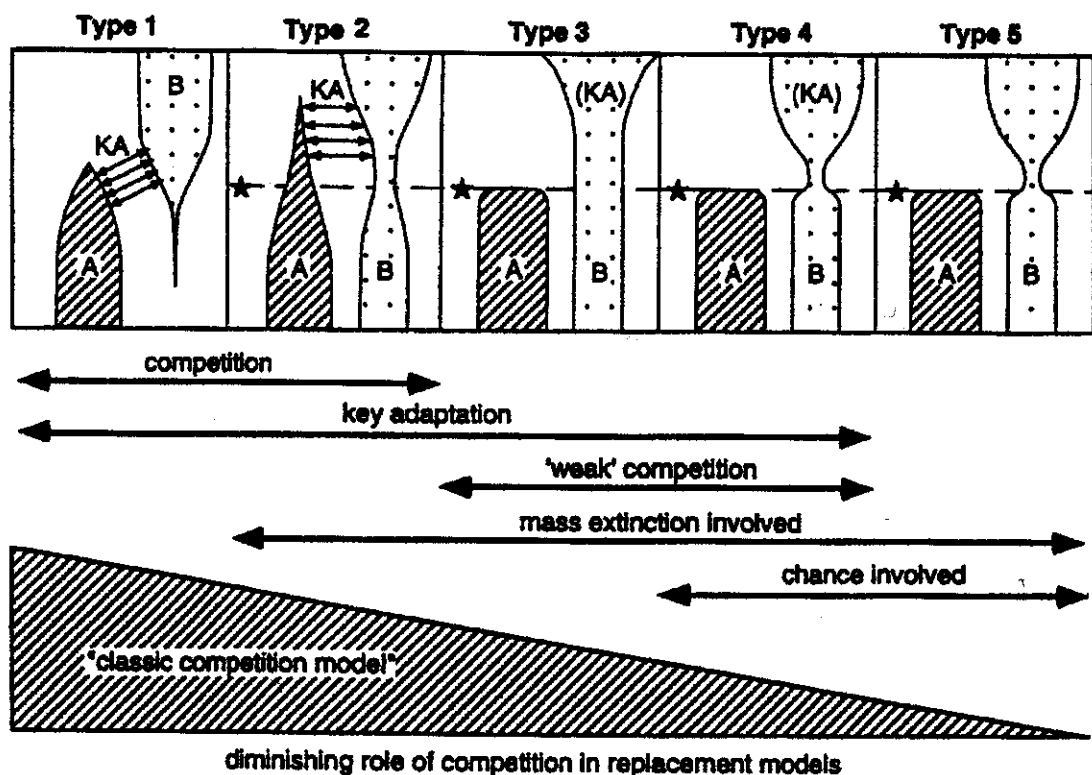
FIGURE 9.   A spectrum of models depicting possible modes of biotic replacement of one clade by another, with the role of competition diminishing, and that of perturbation increasing, from left to right. The star in four of the figures denotes a mass extinction, and "KA" denotes a "key adaptation." Type 1 illustrates a classic "double wedge," and type 5 illustrates a transition contingent entirely on the occurrence of a mass extinction. Intermediate possibilities include scenarios in which a group that is competitively superior is nevertheless impeded until competitively inferior incumbents are decimated by a perturbation. (Reprinted from Benton 1996: Fig. 8.1, by permission of the University of Chicago Press; for further discussion, see Benton 1987, 1991, 1996; Rosenzweig and McCord 1991.)

decrease, and that, when scaled up to geological time, the superior group won out, as measured by complementary changes in constituent taxonomic richness. However, an array of studies have pointed, sometimes unintentionally, to the difficulty of demonstrating that such transitions have actually transpired through competitive displacement. In itself, competitive superiority is difficult to document convincingly, and even if it were possible to make such a case, the geometry of comparative clade shapes rarely, if ever, presents an instance of a definitive double wedge.

These concerns are well-illustrated by the classic case of clams versus articulate brachiopods. Owing to their superficial morphological resemblance, and the recognition that articulate brachiopods gave way to bivalves as major contributors to Phanerozoic benthic marine diversity, it was commonplace to believe that bivalves had outcompeted brachiopods through the course of geological time. Indeed, some workers proffered evidence to suggest that, on a physiological basis, bivalves were competitively superior to brachiopods (e.g., Steele-Petrovic 1979), but a series of studies by Thayer (e.g., 1985, 1986) and Rhodes and Thompson (1993) illustrated the difficulty of making this determination definitively. From the standpoint of their respective diversity histories, Gould and Calloway (1980) showed that there was not the negative correlation in the Paleozoic or post-Paleozoic diversity trajectories of brachiopods and bivalves that would be expected if bivalves had outcompeted brachiopods through the Phanerozoic. Rather, they argued that there was a significant upturn in the diversity of bivalves

and a downturn in that of articulate brachiopods in association with the Late Permian mass extinction, indicating that the extinction was pivotal in governing the post-Paleozoic fates of both groups (see further discussion of mass extinctions, below). Miller and Sepkoski (1988) questioned this view by demonstrating that the per-genus rate of diversification of bivalves was unaffected by the Late Permian mass extinction and by illustrating, with a two-phase coupled logistic model, that bivalve diversification may have been dampened throughout the group's history by interactions with other taxa.

Miller and Sepkoski's (1988) analysis should not be construed as suggesting that bivalves outcompeted brachiopods, however. While one interacting phase (group) in the two-phase model was intended to represent bivalves, the other phase did not represent, from the standpoint of its diversity trajectory, any other clade, and might have appropriately been interpreted as some combination of other taxa on the Paleozoic seafloor with which bivalves might have interacted. Indeed, given this variety of potentially interacting higher taxa, one is left to suspect that the only reason bivalves and brachiopods were singled out in the first place for comparison is their superficial resemblance (Eldredge 1987).

Sepkoski (1996), however, demonstrated elegantly how one might diagnose quantitatively the long-term competitive displacement of one clade by another. Sepkoski et al. (2000) applied this approach to an analysis of the diversity trajectories of cyclostome and cheilostome bryozoans, and developed a solution with a two-phase coupled logistic model that captures most of the important attributes of their Mesozoic and Cenozoic diversity trajectories. This case is compelling because of the evidence that cheilostomes have tended to overgrow cyclostomes where they have encountered one another, both in Recent and fossil cases (McKinney 1992, 1995), suggesting that cheilostomes have historically enjoyed a competitive advantage over cyclostomes. Moreover, application of the coupled logistic model in this instance is unique compared with other studies (e.g., Sepkoski 1984; Miller and Sepkoski 1988): the "younger" cheilosto-

me fauna exhibited turnover rates that were less than those of the "older" cyclostome fauna, and the transition was modeled with these differences incorporated. By contrast, as alluded to earlier, the Phanerozoic-scale transition among evolutionary faunas involved a sequential transition that was the opposite of that exhibited by cyclostomes and cheilostomes: on average, there was a *decrease* in the turnover rates exhibited by successive evolutionary faunas. Thus, in contrast to the Phanerozoic-scale transition among evolutionary faunas, it is not possible to argue, as an alternative to the coupled logistic framework, that the earlier group, the cyclostomes, was simply "weeded out" by perturbations because of its greater evolutionary volatility (see earlier discussion). If anything, the parameters reported by Sepkoski et al. (2000) suggest that the later group, the cheilostomes, was the more volatile.

That said, this is not a classic case of the double wedge because, as recognized by Sepkoski et al. (2000) and Lidgard et al. (1993) and noted by Benton (1996), cyclostome genus diversity has persisted at a rather steady level throughout the Cenozoic. As Lidgard et al. (1993) pointed out, the global diversity trajectories of cheilostomes and cyclostomes may have been affected by a combination of processes played out at different scales.

Donovan and Gale (1990) argued that the post-Paleozoic decline of articulate brachiopods was linked to the early Mesozoic rise of asteroids (the echinoderm variety, not the extraterrestrial kind) that preyed on them. However, Donovan and Gale's own discussion points out the difficulty of demonstrating even today that asteroids like to eat brachiopods. Further, there is little direct evidence of asteroid predation on brachiopods in the fossil record, nor are there even indications that they tended to co-occur in the same assemblages (more extensive critiques of the Donovan and Gale hypothesis are offered by Blake and Guensburg [1990] and Vermeij [1990]).

As with the question of clade-versus-clade dynamics discussed earlier, the Donovan and Gale example illustrates how unlikely it is for the demise of a class-level taxon to be tied to a single kind of ecological interaction. An alternative approach—that of suggesting an

ecological mediation to morphological transitions within groups—has met with much more success. This approach has been perhaps best exemplified by Vermeij's (1977) argument that a suite of morphological transitions exhibited by gastropods after the Jurassic were consequences of the diversification of predators capable of crushing the shells of gastropod prey that were less well protected. This perspective was extended to Paleozoic biotas by Signor and Brett (1994) and was later broadened considerably by Vermeij (1987) to cover a spectrum of cases in marine and non-marine settings, in which morphological arms races are thought to have taken place through geological time between taxa that were "enemies" in the sense that they interacted with one another competitively, or in predator/prey couplets. Vermeij considered these arms races to be a form of "escalation," which he viewed as a pervasive theme of macroevolution.

Vermeij's arguments apply most clearly to morphological characteristics, rather than to taxonomic diversity per se. Despite the failings of cases like that of articulate brachiopods versus asteroids, this is certainly not to say that the taxonomic richness of a given group cannot itself be affected by ecological interactions. However, given the focus on ecology in these instances, it makes much more sense to chart the diversity trajectories of groups that share ecological/trophic attributes, rather than to necessarily limit oneself to evaluating higher taxa linked phylogenetically as monophyletic groups. In many cases, morphological characters that are fundamentally meaningful as phylogenetic indicators are of little ecological significance (e.g., bivalve dentition), and using such characters to chart diversity histories may provide less insight into diversity transitions than using ecological groupings.

Thayer's (1979, 1983) "biological bulldozing" hypothesis constitutes a classic case in which taxa were grouped ecologically across taxonomic boundaries, and the global diversification of one group was shown to be at the expense of another group. In this instance, recognizing that active burrowers ("biological bulldozers") are typically segregated from sedentary suspension feeders on soft-bottom seafloors in the present day, Thayer reasoned that the documented rise of biological bulldozers was responsible for the concomitant decline of immobile suspension feeders on soft substrates (ISOSS), which had dominated Paleozoic seafloors; this transition was initiated in the mid-Paleozoic.

On the face of it, Vermeij's and Thayer's analyses, and others like them, are quite compelling. They are grounded strongly in actualistic evidence, and the actualistic data successfully predict broad transitions that can be observed in synoptic global diversity trajectories. So then why do they make me fidgety? I fidget because, in the documentation of scale-independence, we have sidestepped a scale at which the patterns do not appear to fit our expectations: the local and regional level on timescales of a few to about ten million years. If predators have induced morphological transitions in prey lineages or biological bulldozers have evicted ISOSS, why have we rarely, if ever, observed this happening in the high-resolution stratigraphic records available to us regionally during key global transition intervals (see Brett et al. 1996)? Surely, five million years is sufficient time to effect a morphological change in a lineage or an eviction of an ecological group. Instead, as described earlier, what we observe at local and regional levels are units with relatively little biotic change, bracketed by intervals in which major biotic transitions occur abruptly. Moreover, while this pattern may be accentuated artificially because of the coincidence of turnover intervals with stratigraphic sequence boundaries, the relative abruptness of at least some regional faunal transitions remains even after accommodating these factors (Patzkowsky and Holland 1997).

The biological meaning of this kind of pattern is open to interpretation (Ivany 1996), and it may simply be that rates of evolution are accelerated during these intervals to such an extent that morphological transitions and evictions actually happened, but at rates that were too rapid to be observed in the geological record. Dovetailing on this possibility is the suggestion that the perturbations manifested by the abrupt transitions were required to re-

move incumbents, even in cases when the replacement groups had demonstrable competitive edges over the incumbents (Rosenzweig and McCord 1991).

As alluded to earlier, however, I see a clear, and testable, alternative that likely applies in some instances: that regional perturbations induce net physical changes to regional environmental milieus, and that, following these perturbations, replacement groups become predominant and incumbents are lost not because of interactions, but because of fundamental environmental changes. The example of biological bulldozers versus ISOSS may represent a case in point: clearly, the Paleozoic environments in which ISOSS would have been expected to thrive best were rather different than the muddy substrates favored by deposit-feeding, biological bulldozers. The loss of ISOSS incumbents regionally may have been induced by transitions to muddy substrates; the global shift would thus have been "caused" by the summation of regional changes induced by environmental transitions. A close examination of Devonian strata in New York might reveal, for example, that these two biotas were tracking their preferred lithofacies, which are known to have shifted abruptly on local and regional scales, and that, ultimately, biological bulldozers "won out" in conjunction with the overwhelming progradation of terrigenous sediments associated with the Acadian Orogeny. This is not to say that the entire world became muddy during the Devonian and never went back the other way (see below). But as the history of life illustrates, broad evolutionary transitions are not easily reversed: if a substantial portion of the marine world did become muddy for some protracted interval, say a period or two (e.g., the Devonian and Carboniferous), this would have effected a decline in ISOSS from which it would have been difficult to recover.

In October, 1999, Mike Foote and I were attending a conference in Spain, and we had a chance to talk about some of these issues in detail on a train ride from Valencia to Barcelona. Foote wondered whether, in citing the biological bulldozing example, I was setting up a straw man. As he explained, he was not certain that the bulldozing hypothesis was considered viable anymore, and thus that I was questioning the validity of a hypothesis that had already been dismissed. While I was able to convince him that this was not the case and that, at least to my reading, the bulldozing hypothesis remains as a prominent example of an ecologically mediated global diversity transition, I still had a hard time dismissing the straw man issue in a slightly different context: that I am misinterpreting the general notion of what constitutes a competitive advantage and thus have unrealistic expectations about what we should see when we dissect a global transition into its local and regional components. It might be argued that the ability to thrive in a particular kind of environment constitutes an advantage in itself, and that distinguishing this from a case in which one group displaces another amounts to hairsplitting, given that both may require perturbations to transpire. While the question of whether this matters at all with respect to evolutionary theory is debatable, I will simply assert that it is worth distinguishing between these two alternatives if we have the data at hand to do so: it is worth knowing whether long-term, global biotic transitions can actually be caused by the summation of abrupt, regional environmental transitions, and with a concerted effort, we can do a much more extensive job than we have in the past of mapping the relationship of biotic to physical transitions at a variety of scales.

In a paper published in the tenth anniversary issue of *Paleobiology*, Gould (1985) broadened the theme articulated by Gould and Calloway (1980) in suggesting that mass extinctions collectively constitute an overarching class of macroevolutionary events capable of superseding or undoing evolutionary changes that accumulated during the intervals between them (see also Bennett 1990, 1997). My viewpoint, articulated in this paper and elsewhere (Miller 1997b, 1998), does not really question whether mass extinctions were important mediating events in evolutionary history, but it does remove the firewall between mass extinctions and the so-called background intervals between them (see also Raup 1991, 1992; Martin 1998; Patzkowsky 1999). A closer look at the local and regional data from

which the synoptic, global pattern is constructed reveals that biotic turnover is punctuated by perturbations at a spectrum of geographic scales and that mass extinctions are simply the largest, most globally extensive end-members (see Miller 1998 for additional discussion of this issue). In this sense, the mediation of Phanerozoic diversity is scale-independent in a manner that extends Aronson's (1994; Aronson and Plotnick 1998) interpretation to include physical forcing agents, alongside the ecological and evolutionary processes already categorized in this fashion.

Strolling up to the State Capitol Building, Salt Lake City, October, 1997: The Three (or More) Great Phanerozoic Evolutionary Lithofacies?

While in Salt Lake City for the 1997 Geological Society of America meeting, Dan McShea, Steve Holland, and I walked up the hill to the state capitol building one night to admire the spectacular view. On our walk, we discussed several of the issues recounted herein, and after I admitted to McShea that I was advocating a form of historicism (after he explained to me what "historicism" is), we carried this to its logical extreme spurred on by a question from Holland: Was I suggesting that a global categorization and quantification through time of marine paleoenvironments, if graphed in a style similar to that used for Sepkoski's global diversity curves, would yield a pattern of Phanerozoic transitions paralleling those exhibited by global biodiversity? I confess that my answer at the time was "yes," or at least "maybe." We then discussed how we might actually go about developing the database for such an analysis and convinced ourselves that it would obviously not be an easy thing to do, although it would be interesting to try.

I have come to recognize that it was hopelessly naïve to contemplate this project, not only because it would be a difficult task, but because there is no real reason to expect that the entire history of Phanerozoic diversity can be explained simply by secular changes in the availability of physical habitats. Just as Sepkoski (1996) understood that global competition would not be played out as combat among individuals in two competing groups

through geological time, I concede that the history of Phanerozoic life is not simply the outcome of a battle among myriad "competing" paleoenvironments and geochemistries.

Furthermore, the evidence is overwhelming that biologically mediated pathways have also played major roles in governing the contents of marine biotas throughout the Phanerozoic (e.g., Vermeij 1987; Conway Morris 1998). What I *do* believe, however, is that a broad attempt to exhaustively map Phanerozoic biotic transitions at regional scales in the context of lithostratigraphic and geochemical transitions would improve our wherewithal to choose among alternative mechanisms that purport to explain Phanerozoic biotic transitions.

When we limit ourselves to the global level in seeking explanations for Phanerozoic diversity transitions, we can choose any number of morphological or other features with which to divide up the marine fossil biota into two (or more) mutually exclusive groups. In many cases, regardless of the features chosen, we will end up with a picture of declining diversity for one of the groups and increasing diversity for the other, a pattern that would appear to call for an explanation. However, we can feel much more confident that the global pattern is meaningful if, when we investigate it at the more local levels of individual regions or paleocontinents, we witness the same transition, albeit more abruptly and timed differently from place to place because of differences in the timing of perturbations that permitted the transition to take place (see Rosenzweig and McCord 1991).

Along the way, we must also ascertain whether the diversification patterns exhibited in synoptic compilations transcend scale, as discussed earlier. In the Ordovician and Silurian, for example, there is considerable evidence suggesting that "within-community" (alpha) patterns are at variance with those exhibited at the "between-community" (beta) and global levels (Patzkowsky 1995; Miller and Mao 1998; Adrain et al. 2000).

So, in the end, the simple message of this paper is this: DISSECT, DISSECT, DISSECT. To do so will require the continued development of extensive databases that capture information from the literature already catalogued by

generations of paleobiologists and other geoscientists, combined with a new generation of fieldwork tailored to acquire data from previously uncharted strata or with a higher degree of stratigraphic resolution from some venues than that acquired in the past.

Afterward

A few months before his death, Jack Sepkoski agreed to coauthor this paper. We both recognized that it would be a good vehicle to discuss our different perspectives on global diversity and to identify for readers a palette of research approaches with which to choose among different explanations for Phanerozoic diversity transitions. We never got any further than that, and I cannot honestly say whether Jack would be pleased with anything I have written here. All I know is that every thought I have ever had about biodiversity bears his imprint.

Acknowledgments

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