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Ten years in the library: new data confirm paleontological patterns

J. John Sepkoski, Jr.

Abstract.—A comparison is made between compilations of times of origination and extinction of fossil marine animal families published in 1982 and 1992. As a result of ten years of library research, half of the information in the compendia has changed: families have been added and deleted, low-resolution stratigraphic data have been improved, and intervals of origination and extinction have been altered. Despite these changes, apparent macroevolutionary patterns for the entire marine fauna have remained constant. Diversity curves compiled from the two data bases are very similar, with a goodness-of-fit of 99%; the principal difference is that the 1992 curve averages 13% higher than the older curve. Both numbers and percentages of origination and extinction also match well, with fits ranging from 83% to 95%. All major events of radiation and extinction are identical. Therefore, errors in large paleontological data bases and arbitrariness of included taxa are not necessarily impediments to the analysis of pattern in the fossil record, so long as the data are sufficiently numerous.

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Introduction

Taxonomic data bases in paleontology are compilations of taxa of various ranks, relationships, and regions accompanied by estimates of their times of first appearances and final disappearances in the fossil record. From Phillips (1860) onward, such data bases have been used to investigate changes in diversity, biotic composition, and origination and extinction through life's history, and a number of seemingly robust patterns have been reported (e.g., Sepkoski et al. 1981). However, the information incorporated into all data bases is well known to be imperfect (cf. Raup 1991): only a small fraction of the taxa that ever lived have been sampled (e.g., Teichert 1956; Durham 1967; Raup 1972; Signor 1990), and more fossil material is being described all the time (Raup 1976; Grant 1980). Furthermore, the reported stratigraphic ranges of taxa are often incomplete (Raup 1979, 1989; Signor and Lipps 1982; Strauss and Sadler 1989; Marshall 1990, 1991), and published accounts are sometimes erroneous (Culver et al. 1987; Patterson and Smith 1987, 1989). Finally, the supraspecific taxa in many data bases are often arbitrary and subject to redefinition with new discoveries and changing system-

atic approaches (Patterson and Smith 1987, 1989; Smith and Patterson 1988; Maxwell and Benton 1990). Because there are so many potential sources of error, some workers have rejected all analyses of taxonomic data bases as futile, illustrating only the vagaries of knowledge about the fossil record and not illuminating the tempo and mode of life's evolution. Yet, few analyses have been executed to determine the degree to which actual changes in data bases affect perceived macroevolutionary patterns.

In 1982, I published a data base entitled *A Compendium of Fossil Marine Families* (Sepkoski 1982), which listed stratigraphic intervals of apparent origination and extinction of animal families described from the marine fossil record. These data had been the basis for analyses of taxonomic diversity (Sepkoski 1979, 1981a,b) and subsequently were used for further studies of taxic evolution (e.g., Van Valen 1984, 1985; Kitchell and Carr 1985; Boyajian 1986; Erwin et al. 1987; Gilinsky and Bambach 1987; McKinney 1987; Holman 1989). Of particular note is the controversial hypothesis of periodicity in extinction, induced from statistical analyses of these data by Raup and Sepkoski (1984).

As soon as the manuscript for the 1982 *Compendium* went to press, I began discovering new and old paleontological literature that changed times of origination and extinction and redefined compositions of families or of their orders and classes. After publication of the hypothesis of periodicity, the original data received special scrutiny from taxonomic experts, and embarrassing errors and promulgations of antiquated data were revealed (e.g., Cappetta 1987; Patterson and Smith 1987; Smith and Patterson 1988). For ten years, I have collected these changes from literature sources (with invaluable help from colleagues) and have now published a second edition of the familial compendium (Sepkoski 1992). It incorporates more than 800 new families, deletes approximately 200 old families, and contains over 2000 changes to times of origination and extinction of maintained families. This translates into major changes in the information that was used but a decade ago to make statements about major events in the history of marine life.

How well do these older statements fare in the face of changing data? Below, I compare time series for diversity and for magnitudes of origination and extinction between the 1982 and 1992 versions of the marine familial data. The results are very positive: as was found by Bujak and Williams (1979) and by Maxwell and Benton (1990), the major patterns of taxic evolution are rather insensitive to new fossil discoveries and changes in taxonomic interpretation, indicating that analyses of transitory data can be robust, so long as a large component of the biosphere is being considered.

Nature of Changes in the Data Base

The original 1982 *Compendium* contained nearly 3500 families of marine animals and animal-like protists. Times of origination and extinction were listed in terms of 81 internationally recognized stratigraphic stages spanning 600 m.y. of time, but 13% of the records were resolved only to coarser intervals of geologic series and systems. Over the past ten years, I have increased the taxonomic accuracy and stratigraphic resolution of these

data through continued survey of the new and old paleontologic literature. Changes that have been made, in addition to alterations of suprafamilial classification, fall into four categories (Sepkoski 1992):

1. Deletion of 199 old families that were either invalid or proven to be entirely non-marine.
2. Addition of 838 new families (and distinctive genera not assigned to families) erected on the basis of new discoveries or revisions of older classifications.
3. Correction of more than 1500 stratigraphic ranges that were in error or were subsequently discovered to extend beyond previously documented bounds.
4. Enhancement of the stratigraphic resolution of some 541 records that were previously listed only to the series or system level.

Although these changes emended all taxonomic groups, they were not evenly distributed with respect to taxonomy or stratigraphy. Of the added families, 22% were foraminifera, resulting from the monumental systematic revision by Loeblich and Tappan (1988). This work increased the number of recognized foraminiferal families by nearly 200% and expanded the apparent diversification of the group over the Mesozoic and Cenozoic eras, as illustrated in figure 1. Other groups that experienced substantial (if smaller) additions included radiolarians, sponges, archaeocyathids, gastropods, hyoliths, arthropods, vertebrates, and some problematical taxa. Deleted families were similarly widespread but particularly concentrated among sponges and graptolites, and non-marine families were eliminated from the molluscs, arthropods, and vertebrates.

Corrections of stratigraphic ranges involved extensions and contractions and affected intervals of both origination and extinction. However, the majority of these changes were minor, as shown by figure 2. More than half involved placement of a record in an adjacent stage, and fewer than 20% involved changes of five stages or more. The net effect of these corrections was a small increase in the mean range of maintained fam-

ilies, with the average interval of origination being slightly older and interval of extinction slightly younger. Interestingly, originations were more fluid than extinctions, with changes in 35% of origination records that were originally resolved to the stage level but in only 27% of extinction records.

The reason that extinction records were more robust with respect to changing data is that many are anchored by comparatively brief (one or two stages) extinction events, whereas major radiations are more prolonged, lasting four or more stages. A goodly proportion of the changes in extinction records involved extending ranges toward known intervals of mass extinction. This is illustrated in figure 3, which presents histograms of the numbers of extinctions recorded in the four stages at and before the five great mass extinctions of the marine fossil record (Flessa et al. 1986). In all cases, numbers of extinctions recorded in mass extinction stages are higher in the 1992 *Compendium* than in the 1982 edition (as also is true for the percentage of extinction), and in most cases the number of extinctions is smaller in the preceding stages. The case of the massive end-Permian event is especially dramatic, where intensive study over the past decade, particularly in China (e.g., Sheng et al. 1984; see also Erwin 1990), has extended the ranges of many families to the top of the Permian. This kind of extension is the expectation of Signor and Lipps (1982): incomplete sampling below abrupt extinction horizons will tend to smear back the apparent record of extinctions, but further investigation will expand ranges toward the true point of extinction. Thus, figure 3 can be considered documentation of the action of the Signor-Lipps effect, and illustration of the reality of mass extinctions in the marine fossil record.

Effect on Macroevolutionary Pattern

The documentation of changes in the familial data base above has emphasized non-random effects on taxonomic groups and stratigraphic intervals. These are examples of biases inherent in such data bases. However, when broad patterns of macroevolution over

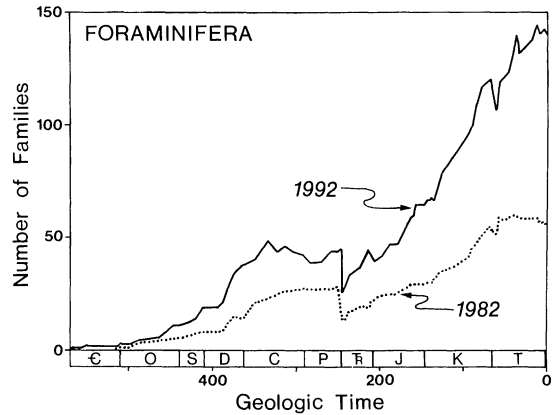


FIGURE 1. Comparison of diversity curves for foraminifera from the 1982 and 1992 editions of the familial compendium. The massive revision by Loeblich and Tappan (1988) greatly increased the number of recognized foraminiferal families and, consequently, their apparent diversity. Although the 1992 curve is broadly similar to the 1982 version, there are important differences. For example, the decline in diversity across the Permo-Triassic Boundary is proportionally smaller and the Mesozoic-Cenozoic diversification is proportionally larger in the 1992 data base. The time scale in this and subsequent figures is from Harland et al. (1990) with minor modifications in the early Paleozoic.

the entire Phanerozoic are examined, the effects of the changes appear more evenly distributed and patterns remain robust. Below, I compare patterns of diversity and of rates of taxic evolution computed from the 1982 and 1992 compendia.

Diversity.—Taxonomic diversity is a cumulative variable, summing numbers of originations and extinctions over time; it is therefore comparatively insensitive to perturbations of the basic data on appearance and disappearance in the fossil record (Sepkoski 1991). This is illustrated by figure 4, which graphs diversity from the two editions of the *Compendium*. The diversity curves are remarkably congruent, despite the large change in data. All major features are the same: the radiations in the Early Cambrian, Ordovician, and Mesozoic-Cenozoic, and the declines in diversity following the end-Ordovician, Late Devonian, end-Permian, end-Triassic, and end-Cretaceous mass extinctions. These are strong signals that show through the noise of imperfect data (cf. Raup 1991). Overall, the goodness-of-fit between the two curves in figure 4 is $r^2 = 0.990$. The

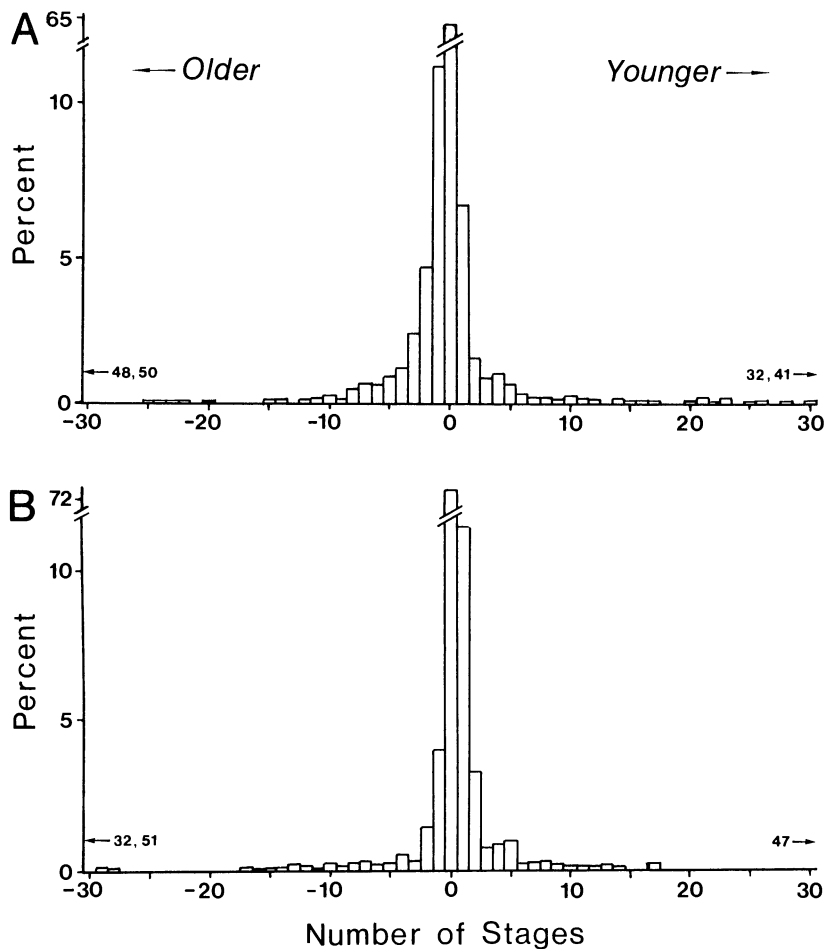


FIGURE 2. Histograms displaying changes in stage-level records for originations (A) and extinctions (B) between the 1982 and 1992 editions of the *Compendium*. The abscissae are the number of stages by which a record has changed, with positive numbers indicating shift to a younger stage, zero indicating no change, and negative numbers indicating shift to an older stage. The histograms show that the majority of records resolved to the stage level in 1982 have not been changed. Among those that have changed, originations show a small tendency toward older stages, and extinctions toward younger stages. Numbers adjacent to arrows are changes falling beyond the limits of the histograms.

general effect of increased numbers of families and extensions and contractions of ranges has been simply to heighten the 1992 diversity curve by an average of 13.5%.

There are differences in detail, however. The upper graph in figure 4 illustrates the percentage of change in apparent familial diversity from 1982 to 1992. All stages exhibit nonnegative change, but increases vary from 0% to 49%. The greatest changes affect the Cambrian, where diversity is low in both data bases. These changes derive from three principal sources: revision of the regular archaeocyathids (Debrenne et al. 1990), extension of

the ranges of many Burgess Shale taxa (Conway Morris 1989), and addition of numerous early Phanerozoic problematica (e.g., Rozanov 1986; Bengtson 1992). Beyond the Cambrian, when diversity is higher, fluctuations in the percentage of increase are less dramatic; several of the spikes that do occur result from the extensions of familial ranges up to mass extinctions. But, in general, post-Cambrian Paleozoic changes tend to fall below the median increase for the Phanerozoic, and Cretaceous-Tertiary changes tend to fall above. This seems, again, to be a function of the huge revision of foraminifera and their

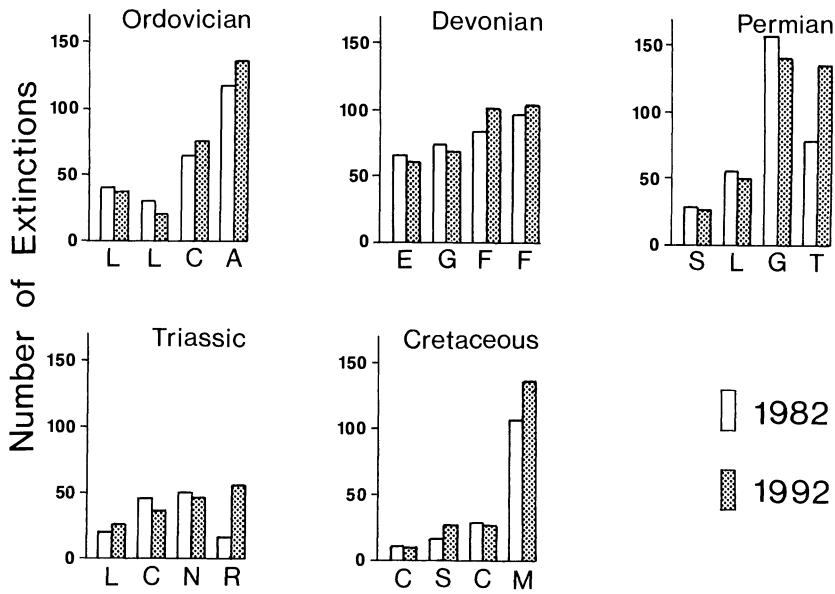


FIGURE 3. Bar graph displays of numbers of extinctions in the 1982 and 1992 compendia in stages encompassing and preceding the five major mass extinctions of the Phanerozoic. Letters below the bars are the first initial of stage names (as listed in Harland et al. 1990); the last stage on the right in each graph is the final stage of the system. In all graphs, the 1992 *Compendium* contains more extinctions than the 1982 edition in the stage(s) encompassing the mass extinctions, and in most cases fewer in the preceding stages.

resulting contribution to the Mesozoic-Cenozoic rise in diversity. Interestingly, however, the 1982 edition of the data exhibits continuing expansion of diversity through the Neogene and Quaternary, whereas the 1992 data show steady state in the short interval following the Late Miocene, possibly reflecting the late Neogene extinction events (Stanley 1984, 1986; Sepkoski and Raup 1986; Vermeij 1986).

Origination and Extinction Rates.—Originations and extinctions are not cumulative variables and therefore should be more sensitive than diversity to changes in taxonomic data. This is indeed the case here, but the correspondence between the 1982 and 1992 data bases is still good, despite a 17% increase in numbers of both originations and extinctions. The relationships for simple numbers of originations and extinctions are illustrated in bivariate plots in figure 5. For originations, the goodness-of-fit between the two data bases is $r^2 = 0.829$, which is high despite change in 50% of the data points. Some of the lack of fit stems from outliers that are easily explained. The most obvious is the unfortunate misdating of the Hunsrückshiefer as Siegenian

(\approx Pragian) in the 1982 *Compendium*, when it is really early Emsian in age. Other positive outliers include the Atdabanian, which has many added problematical taxa; the Middle Eocene, which has added fishes from the Monte Bolca Lagerstätte; and the Danian, which has extended ranges from families previously assigned originations in younger stages. On the negative side is the Kimmeridgian, which is not so easily explained but probably involves a variety of families from the Jurassic radiation that now have originations extended downward.

The correspondence between simple numbers of extinctions (fig. 5B) is slightly better, with a goodness-of-fit of $r^2 = 0.876$. This better fit is consistent with the smaller proportion of changes, noted earlier. The major outliers are the Guadalupian, on the negative side, and the Tatarian (=Djhulfian and Dorashanian) on the positive side; these outliers reflect the Signor-Lipps extension of ranges from the earlier Guadalupian into the overlying Tatarian. Other substantial outliers include the "Rhaetian" (=upper Norian), which has also accumulated range extensions, and the Emsian, which includes the aforemen-

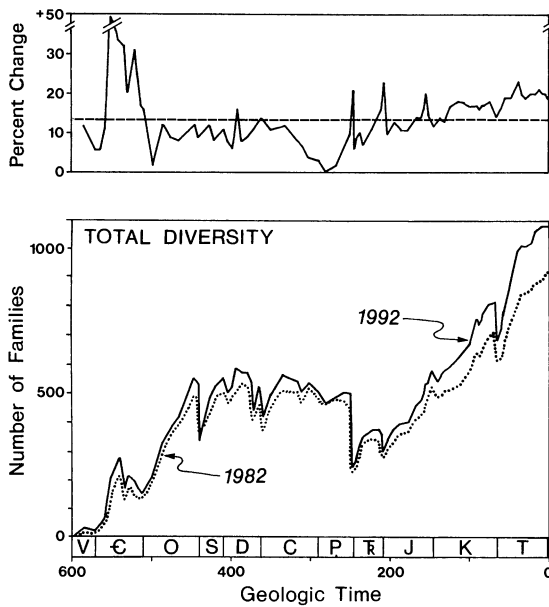


FIGURE 4. Comparison of diversity curves for the total marine fauna computed from the 1982 and 1992 familial compendia. Although the 1992 curve is higher than the older curve, the two are very similar in shape. The graph for the percentage of change shows that the greatest proportional increase in diversity has occurred over the Cambrian and the least over the Permian. (The dashed line in the graph is the median level of change, +13.5%.) The diversity curves were compiled straight from the data, with no interpolations of ranges within orders with discontinuous fossil records (e.g., Octopoda); such interpolation would have increased the apparent change over the Permian.

tioned Lagerstätte. (In most previous analyses of rates of taxic evolution, Lagerstätten taxa were excluded in one way or another; see, e.g., Raup and Sepkoski 1982). With elimination of these obvious outliers, goodness-of-fit between the two data bases increases to greater than 92%.

Plots of numbers of originations and extinctions are influenced to some degree by diversity, the numbers of taxa available to become extinct and to give rise to new taxa. Bivariate plots also do not provide historical perspective on what events of radiation and extinction are preserved between data sets. Figure 6 corrects for both, presenting time series for the percentage of origination and of extinction over time. Data from the 1982 and 1992 compendia are plotted concurrently for comparison, using the stratigraphic intervals of the earlier edition. It is obvious that the matches are strong. The percentage of origination shows the same decline from early to late Phanerozoic in both data bases, with the goodness-of-fit equal to $r^2 = 0.949$; even without the early high percentages, the Silurian to Recent exhibits $r^2 = 0.762$, still a good fit. Differences between the two time series mostly involve Lagerstätten and radiations; for many radiations, the 1992 familial

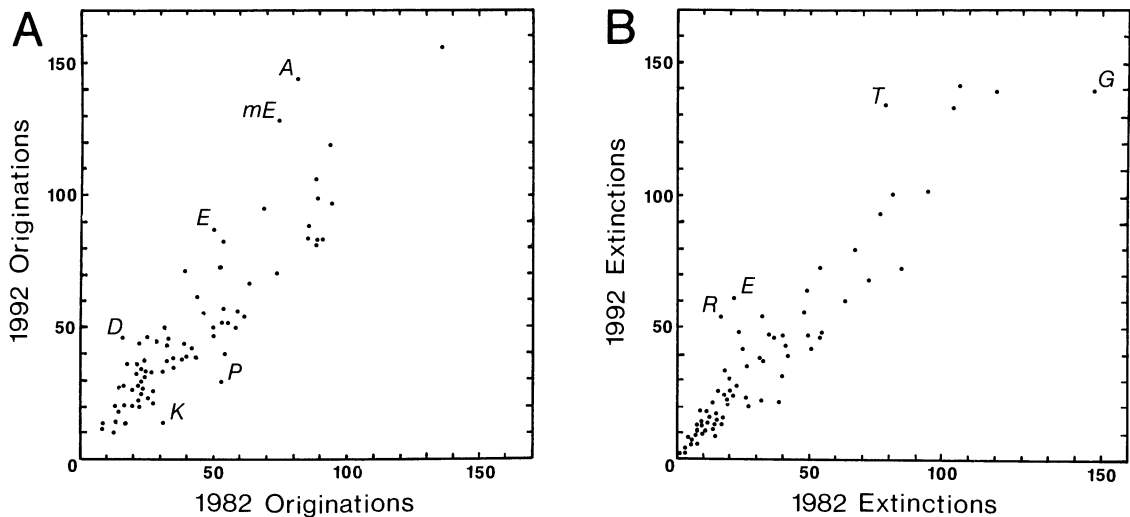


FIGURE 5. Scatter plots for numbers of originations (A) and extinctions (B) per Phanerozoic stage ($n = 78$) compiled from the 1982 and 1992 compendia, using stages in the older edition. Despite massive changes (e.g., fig. 2), there is strong correlation for both originations and extinctions. Points flanked by letters are outliers: A, Atdabanian; D, Danian; E, Emsian; G, Guadalupian; K, Kimmeridgian; mE, Middle Eocene; P, Pragian (\approx Siegenian); R, "Rhaetian" (\approx upper Norian); and T, Tatarian (\approx Djulfian + Dorashanian).

ranges have been extended to earlier stages, the expected complement of the Signor-Lipps effect.

The time series for the percentage of extinction are also basically congruent but with a slightly lower goodness-of-fit of $r^2 = 0.895$. This results in part from the shift of high extinction intensities to stages closer to the ends of extinction events. Without the nine affected stages (Ashgillian, Givetian, Frasnian, Famennian, Guadalupian, Tatarian, Norian, "Rhaetian," and Maastrichtian), goodness-of-fit grows to 91%. The fit increases further with elimination of the mid-Middle Cambrian, which bears the Burgess Shale; a number of taxa in that mother of all Lagerstätten have been discovered in formations assigned to the overlying upper Middle Cambrian (Conway Morris 1989).

Discussion

I believe the results of this exercise are encouraging to those of us who use paleontological data bases to infer generalizations about the history of life. Certainly there can be radical changes in the data being used—both the known fossils that determine first and last appearances of taxa and the interpretation of what specimens constitute taxa. In the examples presented above, 30% of the families had changed over the course of a decade and more than 35% of the remaining families had altered times of origination and/or extinction. Yet, the fundamental patterns of macroevolution remained robust. Real events in the history of life, involving major radiations and mass extinctions, shine through even faulty data. Indeed, this is the legacy of Phillips (1860), who worked with a few thousand fossil species but still recognized the generally low diversity of the Paleozoic and increase in the Mesozoic and Cenozoic eras, as well as the major mass extinctions at the ends of the Permian and Cretaceous periods (Sepkoski et al. 1981; Sepkoski and Schopf 1992).

The results presented here are similar to those of Maxwell and Benton (1990). They examined diversity curves for fossil vertebrates computed from familial compilations produced over the last century. They dem-

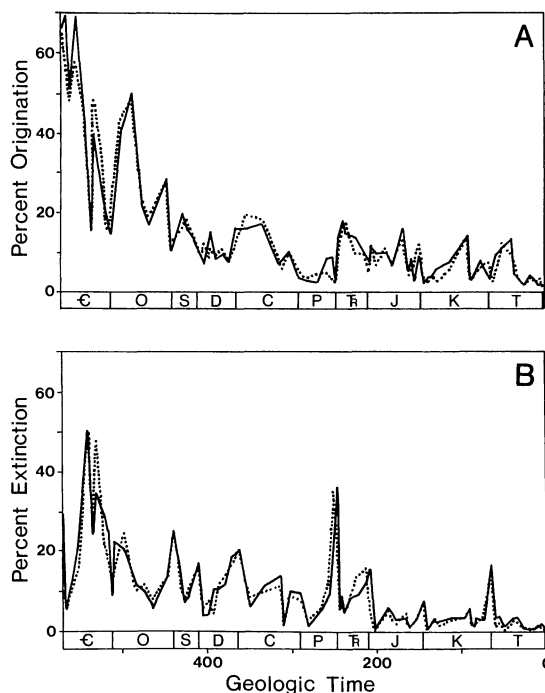


FIGURE 6. Time series for the percentage of origination (A) and extinction (B) compiled from the 1982 (dotted curves) and 1992 (solid curves) editions of the *Compendium* (using the stages of the older edition and all data, without removal of "poorly preserved" families and without range interpolations). There is good correspondence between the curves in both time series, indicating taxonomic data on major radiations and extinction events can be robust with respect to large changes, and macroevolutionary phenomena can be identified with confidence.

onstrated that major radiations, extinctions, and diversity patterns were evident as far back as at least Romer (1933), despite radical increases in numbers of recognized families and changes in taxonomic procedures. The details certainly varied but the principal, long-term patterns were insensitive to changing data.

Thus, large-scale patterns do seem to be robust. But to what degree can data bases be dissected and still yield patterns that can be trusted to reflect aspects of life's history? I do not think that there are any clear-cut rules to apply here (cf. Raup 1991). Specific examples presented above demonstrate how variable portions of the data can be: systematic revision of the foraminifera greatly increased their contribution to diversity; concerted investigation around mass extinctions extended familial ranges toward extinction horizons; and

continued work on Lagerstätten changed patterns for poorly preserved taxa. But, in general, the smaller the taxonomic group, the less specific statements must be. Allmon (1992) presents an example of this for the Turritellidae (Gastropoda): with 51 or fewer taxa (genera in this case), it is impossible to reach strong conclusions about the details of turritellid history, quite independent, I believe, from the problem of arbitrary definitions of the taxa.

All counts of events, such as originations and extinctions—and their composite, diversity—have error associated with them, as the results of ten years of library research indicate. All things being equal, this error varies approximately with the square root of the number of events (Sepkoski and Raup 1986; Sepkoski 1987), which becomes proportionally larger as the number of events becomes smaller (cf. Raup 1991). One should be very careful when making statements about taxonomic groups with comparatively small numbers of constituent taxa, and one should strive to be aware of the preservational and taxonomic effects present even in large data bases.

Conclusions

A comparison has been made between data bases for marine animal families published in 1982 and 1992. Time series of interest are diversity curves and magnitudes of origination and extinction. The 1992 data base incorporated only half the information in the 1982 publication, with many families deleted, new families added, and stratigraphic ranges of many maintained families altered. Despite this great change in data, the patterns derived from the taxonomic data bases proved resilient: diversity curves over the whole of the Phanerozoic were similar, and time series for origination and extinction matched in all major aspects. These results suggest that errors and changes in paleontological data bases are not fatal: statistical patterns in which signal exceeds noise can be perceived despite continuing discovery of new fossils and evolving perceptions of taxonomic identity.

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