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## Patterns of generic extinction in the fossil record

David M. Raup and George E. Boyajian

*Abstract.*—Analysis of the stratigraphic records of 19,897 fossil genera indicates that most classes and orders show largely congruent rises and falls in extinction intensity throughout the Phanerozoic. Even an ecologically homogeneous sample of reef genera shows the same basic extinction profile. The most likely explanation for the congruence is that extinction is physically rather than biologically driven and that it is dominated by the effects of geographically widespread environmental perturbations influencing most habitats. Significant departures from the congruence are uncommon but important because they indicate physiological or habitat selectivity. The similarity of the extinction records of reef organisms and the marine biota as a whole confirms that reefs and other faunas are responding to the same history of environmental stress.

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### Introduction

Newell (1952), Simpson (1953), Schindewolf (1962), Müller (1961), Valentine (1969), and a few other paleontologists of the 1950s and 1960s pioneered the use of data compiled from the monographic literature to search for patterns in the history of life. These workers were mindful of the pitfalls of using compilations of statistical data, and most of the early papers contained extensive discussions of the errors, biases, and uncertainties inherent in this kind of research. Following one such discussion, Newell (1952) concluded with the following statement of optimism:

“Naturally, strict evaluation of these and other sources of error are at present impossible. Nevertheless, the regularity of certain trends and patterns exhibited by the data appear to be independent of any of the more obvious sources of error. I believe that we can draw from these data useful clues regarding the facts of invertebrate evolution.” (p. 372)

Although many paleontologists still doubt that massive statistical compilations of taxonomic data are suitable research tools (for example, Koch 1978; Culver et al. 1987), the optimism of Newell, Simpson, and others may have been justified because the patterns they saw in rather primitive datasets have, for the

most part, been substantiated by analyses of more comprehensive compilations.

In this paper, we will present an analysis of about 20,000 genus-level extinction records drawn from the new data base being developed by J. J. Sepkoski, Jr., to whom we are indebted for permission to use the data (for a description of the data base, see Sepkoski 1986). The study will thus extend the work of McKinney (1985, 1987) and others who have analyzed Sepkoski's (1982) family-level compilation.

### The Problem

Does the fossil record of extinction in the Phanerozoic show a consistent, repeatable pattern, or is it a confused amalgam of signals produced by many independent evolutionary histories? The question is appropriate whether the groups are defined taxonomically, ecologically, geographically, or physiologically.

We have only limited information on this fundamental and important issue. A number of claims have been made in specific cases and many of them are well-supported by rigorous analyses. It is generally agreed, for example, that large body size increases the risk of extinction. The extinctions of large reptiles at the end of the Cretaceous and of large mammals in the late Pleistocene are prime

TABLE 1. Principal taxonomic groups and subgroups analyzed in this study. Numbers of genera refer to the unpublished Sepkoski data base as it was in July of 1987.

	Number of genera	Median percent extinction per stage
Foraminiferida (all)	1,095	8.3
Anthozoa		
Rugosa	675	46.9
Scleractinia	259	8.3
Tabulata	262	41.7
Others	34	
Total	1,230	23.4
Bryozoa (all)	791	11.6
Brachiopoda		
Atrypida	119	36.0
Orthida	270	52.9
Pentamerida	139	50.0
Rhynchonellida	419	42.9
Spiriferida	422	29.8
Strophomenida	708	41.7
Terebratulida	325	40.0
Others	167	
Total	2,569	35.4
Bivalvia		
Hippuritoida	116	40.4
Pterioida	343	10.3
Veneroida	395	8.7
Others	357	
Total	1,211	11.0
Gastropoda		
Archaeogastropoda	500	10.4
Mesogastropoda	562	9.3
Neogastropoda	438	11.1
Others	140	
Total	1,640	12.4
Cephalopoda		
Nautilida	174	38.2
"Ammonoidea"*	2,113	74.3
Others	969	
Total	3,256	61.2
Echinodermata		
Crinoidea	681	31.3
Echinoidea	371	15.5
Others	496	
Total	1,548	26.2
Arthropoda		
Trilobita	1,968	53.4
Others	1,398	
Total	3,366	26.8
Fishes (all)	943	20.6
Reptilia and Mammalia (all)	287	80.0
All other groups	1,961	
All stage-level genera	19,897	28.8

\* "Ammonoidea" defined as including the orders Anarcestida, Clymenida, Goniatitida, Prolecanitida, Ceratitida, Phylloceratida, and Ammonoidea.

examples, but many cases have been verified among marine invertebrates as well (for review, see LaBarbera 1986). During the terminal Cretaceous event, detritus feeders seem to have been favored over those organisms dependent on living plant matter (Sheehan and Hansen 1986). And Jablonski (1986a) has shown that survival of genera is favored by several traits (species-richness, planktotrophic development, and broad geographic range of constituent species) between mass extinctions but not during mass extinctions.

These and other examples suggest that extinction is a highly selective process, so that one should not expect to see a consistent extinction profile for an interval of time unless the samples are ecologically or physiologically homogeneous.

On the other hand, many workers have noted similarities in the extinction records of quite disparate groups. In one of the earlier studies, Newell (1952) concluded:

"Analyses of the better records of the fossil invertebrates show that rise and fall in apparent evolutionary activity is not at random. In a large proportion of the major groups, times of low evolutionary activity tend to coincide." (p. 385)

In spite of Newell's work, there seems at present to be a fairly strong consensus among paleontologists that the extinction record is indeed highly selective, especially where taxonomic groups are compared. One often hears statements like "My group was not affected by [this or that] mass extinction." Although such statements are doubtless true, at least at some scale, it is important to refine and verify them with synoptic analyses of the large data bases now available. It may well be that both sides of the issue are correct because selectivity may be present at some scales but absent at others.

### Data Base

As of July 1987, the unpublished Sepkoski dataset for fossil marine genera contained about 28,000 entries. The present analysis is based on the approximately 20,000 of these that have stratigraphic ranges with stage-level or better resolution.

The Sepkoski compilation is based primarily on reports in the source literature, but it has been supplemented and corrected by personal contributions by a number of paleontologists and biostratigraphers. The data base is far more accurate and fully developed than any other of its kind. In particular, it is a vast improvement on compilations based solely on the *Treatise on Invertebrate Paleontology* or *The Fossil Record* (Harland et al. 1967).

The sample is inevitably dominated by certain major groups of well-skeletonized marine invertebrates (including protists), which make up about 94 percent of the total. Table 1 lists the major taxonomic groups in the stage-level sample, with numbers of genera in each. Several subgroups, also listed in Table 1, were treated separately in some of the analyses. Other subgroups, such as the inarticulate brachiopods and graptolites are of interest but do not contain sufficient genera with stage-level stratigraphy to make separate treatment possible.

### Extinction Metric

Several related measures of extinction intensity have been used in past statistical studies. The most common are:

- (1) Number of taxa becoming extinct in a stratigraphic interval, such as a sub-stage, stage or series,
- (2) Percent extinction in an interval,
- (3) Number of extinctions per million years ("total rate"), and
- (4) Percent extinction per million years ("per-capita rate" or "probability of extinction").

In a surprising number of cases, all four metrics yield similar patterns (see Sepkoski 1986, for comparisons).

Ideally, those metrics which are normalized for absolute time (3 and 4, above) should be preferred, but the extreme uncertainty in estimating stage durations adds intolerable error. For example, if the time-normalized metrics are used for the Coniacian Stage of the Late Cretaceous with the Harland Time Scale (Harland et al. 1982), the Coniacian yields the largest mass extinction of the Phanerozoic. There is no independent evidence

for such an event. The same sorts of problems arise with other time scales (Odin 1982; Palmer 1983; Snelling 1985).

The choice of metric adopted here is simple percent extinction (2, above). This normalizes for standing diversity (number of genera available for extinction), but not for absolute time. The lack of time normalization is accommodated by using a time scale (below) that minimizes variation in stage length.

### Time Scale

The conventionally recognized stratigraphic stages of the Phanerozoic will be used for this analysis, but with an important difference: several of the shorter stages have been combined to reduce the effect of not normalizing for stage duration. The following groups of stages were combined into single units:

Pliocene and Pleistocene  
 Turonian, Coniacian, and Santonian  
 Induan and Olenekian  
 Djulfian and Dorashanian

The result is a time scale of 74 units with a mean duration of about 8 m.y. and minimal variation (standard deviation = 3.7 m.y.).

### To Cull or Not to Cull?

In any analysis of the sort attempted here, the signal-to-noise ratio can be increased by removing certain classes of uncertain or questionable data. This has already been done in Table 1 by eliminating the 8,000 genera for which the time of origination and/or extinction is resolved only to the series or system biostratigraphic level. But further culling could be done to minimize problems caused by special preservational situations (Lagerstätten such as the Solnhofen Limestone), the Pull of the Recent (Raup 1979a), and certain kinds of taxonomic uncertainty.

Given the stage-level generic ranges, the following four sampling regimes are reasonable:

- (1) FULL SAMPLE: 19,897 genera (all stage-level records)
- (2) EXTINCT TAXA ONLY: 17,269 genera (to eliminate the Pull of the Recent)

- (3) MULTISTAGE RECORDS ONLY: 9,834 genera (to eliminate many of the effects of Lagerstätten and also of oversplitting of taxa in some formations)
- (4) MULTISTAGE RECORDS FOR EXTINCT TAXA ONLY: 7,566 genera (to combine 2 and 3, above)

Each of the culling systems has some merit, but the costs in sample size are high.

In the present case, most of the analyses have been run with all four alternatives with the somewhat surprising result that the extinction patterns differ in no significant way. For example, Lagerstätten such as the Solnhofen can be eliminated by using only multistage records (genera lasting at least two stages). The Solnhofen contains many short-ranging genera because preservation is better than in older and younger rocks, but the number of these genera is small relative to the total dataset and their removal has little effect. This will be illustrated (below) for the bivalve record. In view of this experience, preference is given to the first alternative, the full sample of stage-level ranges.

### Special Problems

As has been pointed out by many previous authors, analysis of taxonomic compilations poses difficulties of uncertainty and bias. Some of these have already been discussed (above) but four additional problems deserve special attention.

*Use of supraspecific taxonomic units.*—The ultimate objective of any study of extinction should probably be to assess mortality at the level of species. However, in the present state of our knowledge of past life, rigorous work at the species level can be done only in certain restricted situations where preservation is ideal and time control excellent. Research at this scale is valid and important for some extinction events, such as the Frasnian–Famennian boundary (Devonian) and the Cretaceous–Tertiary boundary. But it is impossible to do synoptic studies for large segments of geologic time on this basis because the general quality of the species record is not good enough.

Therefore, we must use *proxy* data at a higher level and interpolate back to the species level. Families and genera are used most often as proxies with the justification that patterns of extinction and diversification in these units have been observed to track species patterns (Sepkoski et al. 1981). We need not know precisely what a genus or family is as long as there is an operational correspondence between rises and falls in species, generic, and familial patterns.

Moving to supraspecific taxa dampens the extinction signal, of course. Because all members of a genus must die out before a generic extinction is recorded, only some of the species extinctions for a given time interval are reflected in generic data. For example, in the latest Cretaceous, 70–80 percent of the marine species went extinct (using the reverse rarefaction method of Raup 1979b), but only 47 percent of genera and 14 percent of families died out.

*Variable quality of taxonomy.*—The products of taxonomic research contain many problems and uncertainties familiar to all systematic biologists and paleobiologists. Some groups are over- or under-split, and concepts of the genus and family vary greatly. A genus in one group may be equivalent to a family in another group. Any taxonomy is subject to “monographic bursts”—times when large numbers of new taxa are discovered because of the efforts of a single worker or project. In spite of these difficulties, overall patterns change remarkably little in “monographic” time. Grant (1980), for example, compared brachiopod diversity patterns as seen in 1969 and 1979, a period of exceptionally active taxonomic research. The total number of genera had increased substantially in the ten years but the basic shape of the diversity curve changed very little: the peak diversities remained in the Devonian, Ordovician, Permian, and Jurassic, in that order.

*Paraphyly.*—Many higher taxa currently in use would not exist if cladistic taxonomy were used. Many groups in the Sepkoski data base are certainly paraphyletic in the sense that they gave rise to descendent groups of the same rank, rather than becoming extinct without issue. The classic example is the case

of dinosaurs at the order level: if birds evolved from dinosaurian ancestors, then the dinosaurs did not become extinct at the end of the Cretaceous. If all paraphyletic groups were eliminated from taxonomy, extinction patterns would certainly change (Patterson and Smith 1987).

The problem of paraphyly is far more severe for families and orders than for genera, at least in the present state of knowledge. For this reason, among many others, data bases for genera are preferable to those for families.

Furthermore, one can argue that the paraphyletic genus serves effectively to define a group of species occupying a small portion of morphospace and that the disappearance of such a group is a true indicator of the extinction of closely similar species—whether or not members of that group evolved into forms elsewhere in morphospace (Sepkoski 1987). By this reasoning, it may even be that paraphyletic taxa are *better* proxies for species extinction than truly monophyletic taxa because they yield a much less dampened indication of extinction at the species level.

*Volatility.*—Almost all synoptic studies of extinction have shown that some taxonomic groups have consistently higher or lower extinction rates than others. We will refer to this as variable *volatility*. Much has been made of the question of whether mammals have inherently higher evolutionary rates than bivalves because the former are observed to have shorter-ranging taxa than the latter. And differential volatility is certainly rampant among marine invertebrates, and this has been evaluated most recently by McKinney (1985, 1987). The main problem is that it is rarely possible to know for sure whether the observed differences are biological or are merely artifacts of differing taxonomic practice.

It should be emphasized that the term *volatility* is used here to express *average* extinction intensity (mean or median) of a group and *not its variability* within that group. Thus, mammals have a higher volatility than bivalves whether or not they exhibit greater stage-to-stage variability in extinction intensity.

Because our purpose here is to compare *patterns* rather than *magnitudes* of extinction, we

TABLE 2. Results of comparisons of percent extinction in each stratigraphic stage with the mean of the subjacent and superjacent stages.

Stages where all nine invertebrate groups (Table 1) have percent extinction higher than the mean of the subjacent and superjacent stages for those groups:

Ashgillian	Maestrichtian
Stephanian	Upper Eocene
Pliensbachian	Middle Miocene

Stages where eight of the nine groups show higher percent extinction:

Tremadocian	Norian
Arenigian	Tithonian
Wenlockian	Cenomanian
Visean	

Stages where all nine groups show lower percent extinction:

Llandovery	Campanian
Asselian	Danian
Hettangian	Upper Oligocene
Aalenian	

will remove much of the effect of differences in volatility by subtracting the sample median from the extinction value for each stage. This will be explained more fully as the results are presented.

## Results

The most striking result of the analysis of the 19,897 generic ranges is that the various taxonomic groups and subgroups show highly similar extinction profiles for the Phanerozoic. This can be documented in several ways. For example, Table 2 lists six stratigraphic stages for which all nine major invertebrate groups have extinction intensities higher than the mean of the subjacent and superjacent stages for those groups. That this uniformity should be found in as many as six of the 74 time intervals is well beyond chance expectations. Not surprisingly, all six are times of well-known extinction peaks. Note, however, that no late Devonian, late Permian, or late Triassic stages are included. This is because of real or preservational smearing of these mass extinctions.

The second list in Table 2 gives seven stages where all but one of the nine groups are consistent, and this also suggests a non-random pattern. The third list in Table 2 includes the

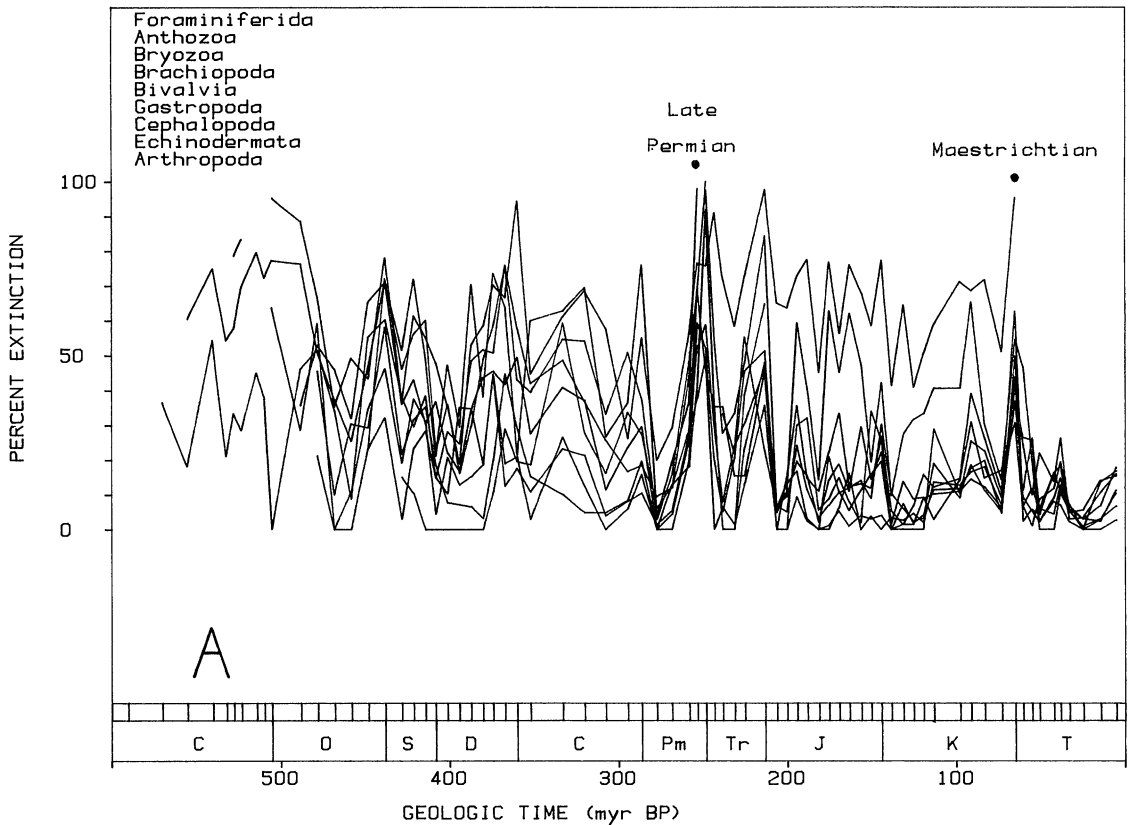


FIGURE 1. Extinction profiles for nine major Phanerozoic groups (sample sizes listed in Table 1). Only stages with at least ten genera in a group are considered. A, Raw data. B, Profiles adjusted downward by subtracting the median value of each profile. The adjustment serves to eliminate much of the effect of group-to-group differences in volatility (average extinction intensity).

seven stages where extinction values are uniformly lower than the mean of subjacent and superjacent stages. Most of these follow stages with unusually high extinction and thus are to be expected.

Figure 1A is a composite plot of the extinction profiles for the nine major invertebrate groups. The ordinate is percent extinction (per stage). The nine extinction profiles present a rather confused tangle of crossing lines wherein only the largest mass extinctions can be seen clearly. Much of the confusion is caused, however, by differences in volatility.

The same data are plotted in Fig. 1B, with the position of each profile adjusted downward by subtracting its median. Thus, a point at zero is at the median for its group. Median-plotting does not change the shape of the extinction profiles; it only moves them down on the graph. The median, rather than the mean, is used because most groups show right-

skewed distributions of per-stage extinction intensity (more low values than high values).

At first glance, Fig. 1B still shows a confusion of nine different profiles. But on closer inspection, a clearly non-random pattern can be seen. The Late Permian, Late Triassic, and Maestrichtian extinction events are pronounced and sharp, affecting all groups. Most of the events in the Mesozoic and Cenozoic used by Raup and Sepkoski (1984) to document the periodic nature of extinction can be seen, but the regular spacing is not obvious because of the coarse time scale and lack of filtering (see Sepkoski 1986: fig 3 for comparison). A few well-known extinctions in the Paleozoic can be seen, but they are considerably smeared.

Some statistical perspective can be gained by comparing Fig. 1B with random samples of the total dataset. In Fig. 2, extinction profiles are shown for ten samples of 1,000 genera, each drawn at random from the full da-

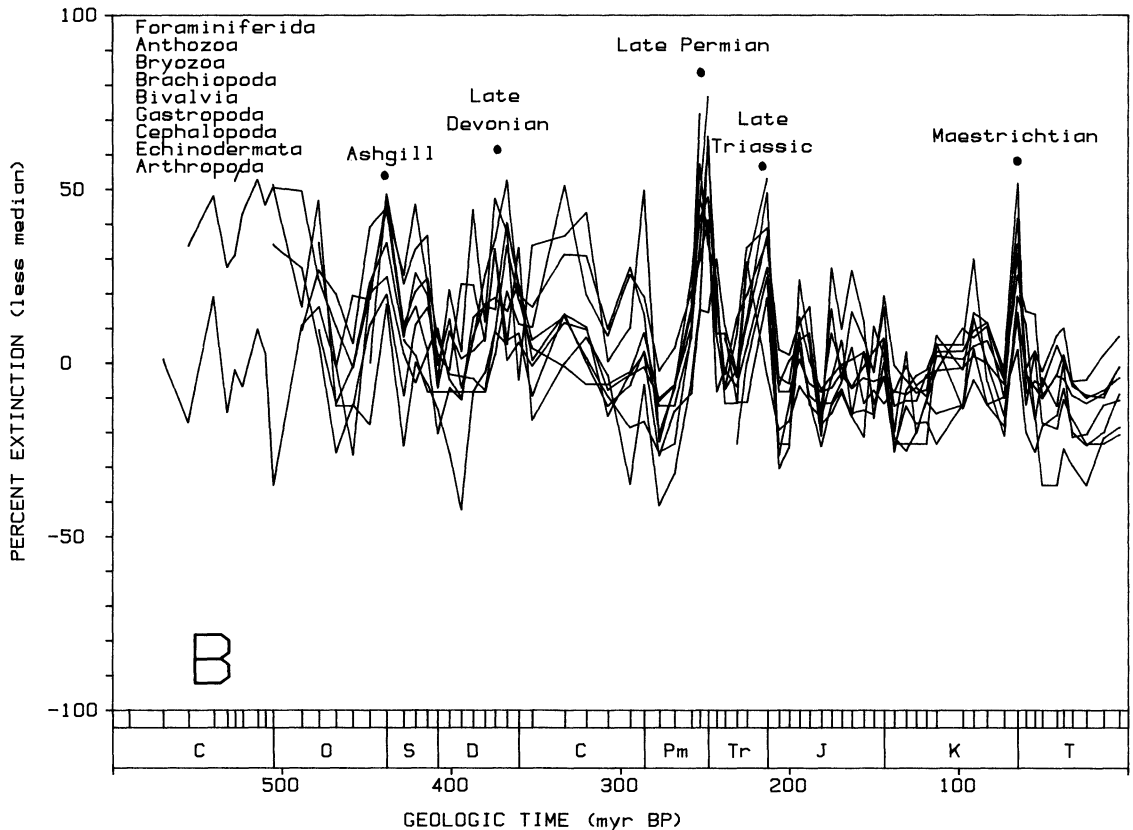


FIGURE 1. Continued.

taset of 19,897 genera. In the simulations, the array of profiles is ragged due to the vagaries of sampling, but major extinction events still show clearly. The clarity of these events weakens in the Paleozoic due to lower standing diversity and a consequent increase in random sampling error.

With the benefit of the random samples for comparison, Fig. 1B shows two opposing but compatible features: (1) the nine invertebrate groups follow approximately the same profile for the Phanerozoic as a whole, and much of the variation in detail may be attributed to sampling error, and (2) the taxonomic groups are more different from each other than would be expected by chance in a random sampling regime (from the fact that the scatter is greater in the real records than in the random samples). Thus, at this scale, we see the *absence* of selective extinction in the similarity of profiles and the *presence* of selective extinction in the larger than expected group-to-group differences.

Figures 3–8 explore the above relationships in more detail. In these figures, only stages with at least ten genera of the group in question are plotted. Figure 3A is a plot of extinction in the bivalve sample compared with the profile for all other genera in the full dataset. The bivalve profile is shown as a band with a width of two standard errors (counting error estimated by the method described by Raup and Sepkoski 1986: note 7).

If the data for Fig. 3A had not been adjusted by subtracting medians, the bivalve profile (median = 11.0 percent) would have been consistently below the “all others” profile (median = 25.7 percent) because of the lower volatility of bivalves. The shapes of the profiles would have been the same, of course, as those seen in the figure. Note that the “all others” median (25.7) is lower than that shown for the total sample in Table 1 (28.8), because the former lacks the influence of early Paleozoic groups, such as trilobites, that have unusually high extinction values.

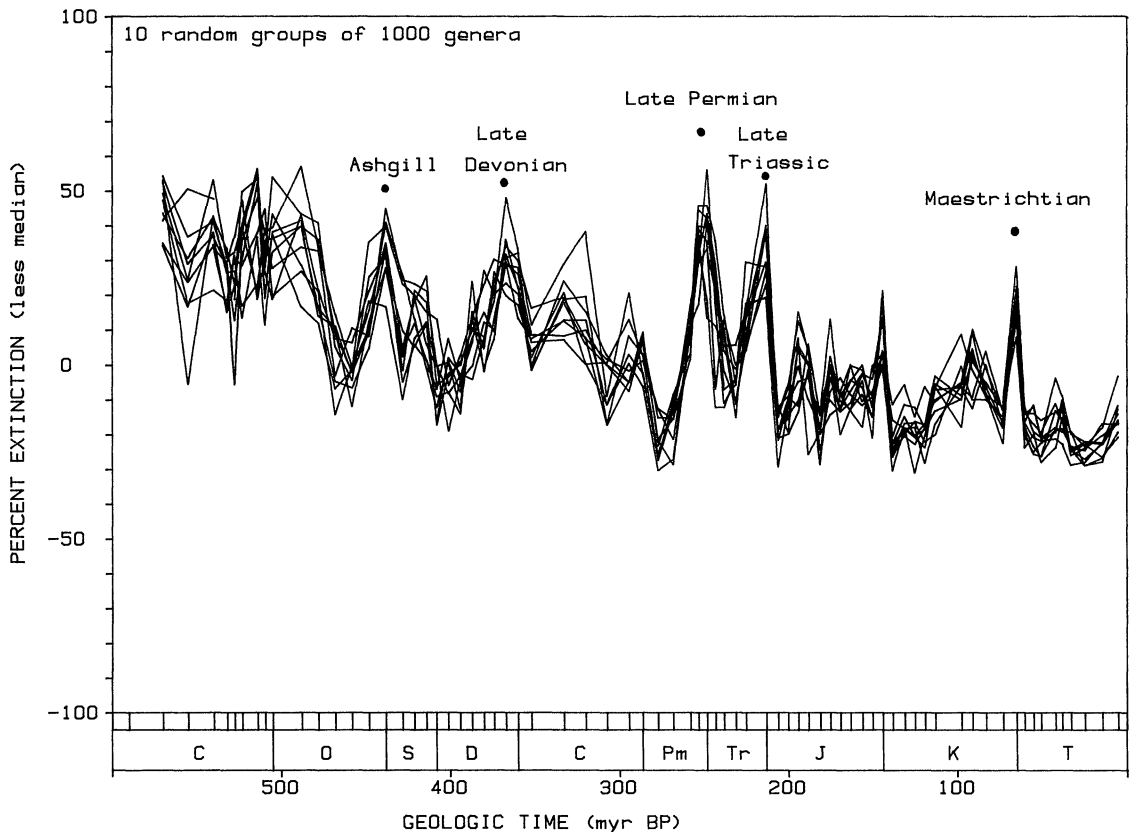


FIGURE 2. Extinction profiles as in Fig. 1B for ten samples of 1,000 genera chosen at random from the total dataset.

The two profiles in Fig. 3A are remarkably similar, with most highs and lows matching and with only minor differences in heights of peaks. In a few places, however, there are substantial departures such as the absence of a bivalve peak in the Viséan and the presence of a bivalve peak in the Aptian.

Figure 3B is the same as Fig. 3A except that only multistage records are considered, thus reducing the total available sample from 19,897 to 9,834 genera. The culling process has changed the details of the pattern, but the basic correspondence between the bivalve record and that of the rest of the sample is unchanged. Note that in Fig. 3B, the Viséan peak has shifted to the next younger stage (Serpukhovian) and the Aptian peak is much weaker. The unculled dataset (Fig. 3A) is probably more meaningful for the present purpose because of the much larger sample size.

To emphasize the correspondence seen in Fig. 3, a scatter plot of the raw extinction data for bivalves and all other genera (using the full dataset of Fig. 3A) is presented as Fig. 4 (one point per stage). This shows (1) the generally lower extinction intensity for bivalves and (2) the strong correlation between the two sets of data ( $r = 0.78$ ). That is, apart from the lower volatility of bivalves (for whatever reason), the bivalve sample of 1,211 genera is an excellent predictor of the extinction record of the total biota.

Figure 5 compares the extinction profile of brachiopods with that of all other genera. Again, the correspondence is striking. The brachiopod profile is lower than that for the other genera in the Cambrian and Ordovician, but this is largely because the "all others" sample is dominated by trilobites with high extinction values. The brachiopod peaks in the Mesozoic are high and sharp, and this

is due to the fact that brachiopods, like cephalopods, have a frequency distribution of extinction intensities very different from that of the total sample. It should be noted, however, that the Cenomanian peak for brachiopods is not only higher than that for other genera, but it is higher than the brachiopod Maestrichtian peak. These and other differences further establish the presence of non-trivial differences despite the fundamental similarity of group patterns.

To explore the brachiopod case in more detail, Fig. 6 shows the profile for one order, the Spiriferida, compared with all other genera in the dataset. The spiriferids track the total sample almost perfectly. In Fig. 7, intergroup tracking is shown by the profiles of the seven brachiopod orders having sufficiently large samples for analysis. In this case, most of the differences in profile can be ascribed to random sampling error.

### Statistical Significance of the Results

It is tempting to build statistical tests to determine which of the similarities and differences seen among the extinction profiles are "significant." We have avoided this, however, because so many unwarranted assumptions would be required. For example, when frequency distributions of extinction intensities are constructed for the several groups, it is clear that they differ in important ways. Cephalopods have a modal percent extinction much higher than zero, whereas most (but not all) other groups have right-skewed distributions such that most values are low. This can be seen also at the family level in McKinney's analysis (1987: table 2). Because of the differences in skewing, results of standard parametric testing could be misleading.

The situation in cephalopods (and a few other groups) is probably a result of their higher volatility; their distributions are what one would expect for species rather than genera. But this does not help solve the statistical problem. It is possible that intensive bootstrapping could produce satisfactory tests, but this has not been done. Therefore, the assessments of Figs. 3–8 are frankly subjective—although aided by the error bands shown in some of the plots.

Another kind of statistical problem concerns intergroup correlations of extinction intensity, such as that in Fig. 4. The correlation in Fig. 4 ( $r = 0.78$ ) is indeed strong and with 62 points would pass conventional tests of statistical significance. But to perform such tests would be to presume several conditions which are definitely absent. Most importantly, Fig. 4 constitutes the relation between two Markovian time series and, as shown by Yule (1926), this usually yields apparently significant values of the correlation coefficient even in the absence of cause and effect. In this case, therefore, we must be satisfied with the rather obvious conclusion that extinction values in a group seem to track those in the total sample.

### Interpretations

The simplest and most obvious interpretation of the data presented thus far is that most taxonomic groups do indeed "march to the same drummer" and that departures from consistency are interesting but relatively minor. This is a surprise in view of the general consensus among paleontologists that the extinction record is dominated by taxonomic selectivity. At the scale of the present analysis, at least, the common saying "My group was not affected. . . ." is not sustained in most instances.

But before accepting this interpretation, we must consider several alternative explanations, as follows.

*Time scale problems.*—Because the 74 time intervals have varying durations, despite the lumping of short stages, it could be that extinction peaks are being produced in the long intervals, merely as an accumulation of background turnover. Although this may be a minor element, it is unlikely to be significant because of the lack of statistical correlation between interval duration and extinction (Raup and Sepkoski 1984; Raup 1986).

*Heterogeneous taxonomic groups.*—The class and order level groups being considered here are primarily genealogical and only secondarily ecological, biogeographic, and physiological groups. It is conceivable that these large groups are so heterogeneous that they approximate random samples of the whole

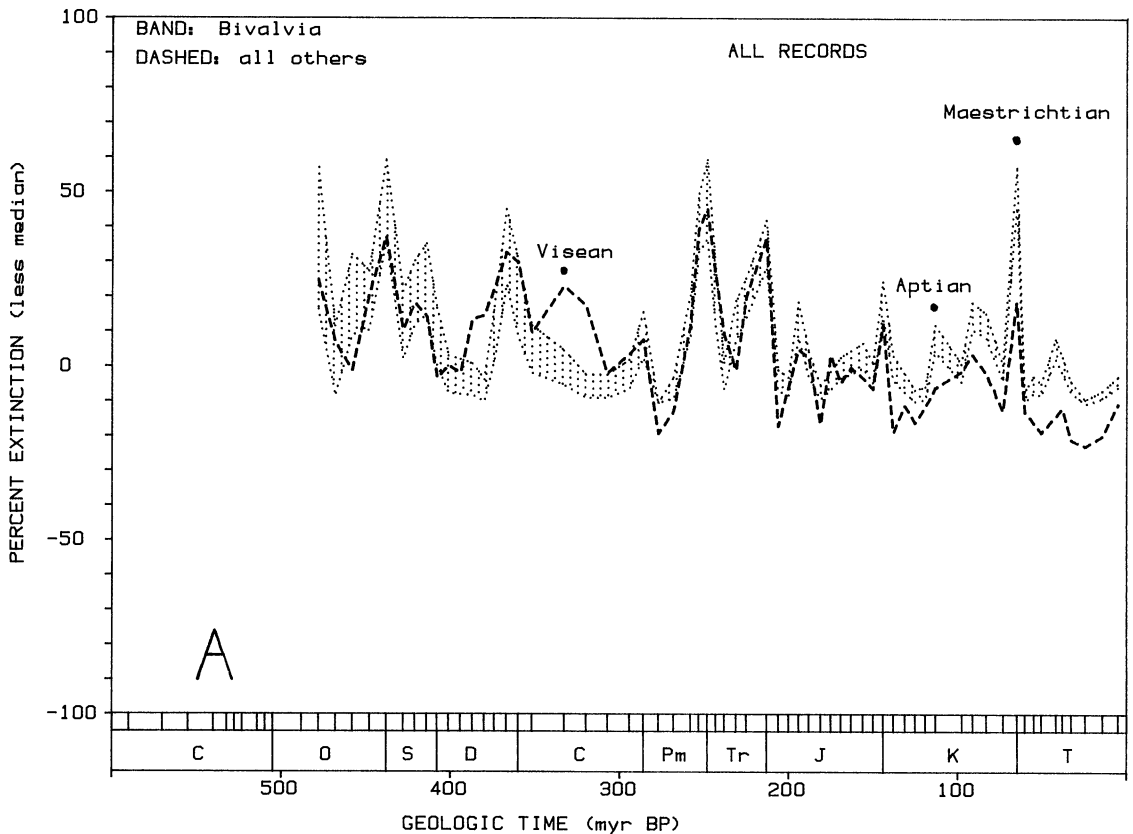


FIGURE 3. Bivalve extinction compared with that for all other genera in the sample. Only stages with at least ten bivalve genera are considered. The band for the bivalve profile has a width of two standard errors. A, Full sample. B, Multistage genera (those with ranges of more than one stage).

dataset and thus show similar extinction profiles.

Although this may be an element, it is unlikely to play a significant role. This can be argued on the basis of plots such as Fig. 6 where a homogeneous group, the order Spiriferida, has an extinction profile highly similar to that for all other genera.

Figure 8 shows a further test. Here, two of the most different groups are compared: the brachiopods are sessile, filter-feeding benthos, and the "ammonoids" (see Table 1 for definition) were swimming, non-filter-feeding organisms in a different phylum. The two profiles are still similar and display about the same kinds of differences observed in other comparisons.

*Similar preservational histories.*—It could be argued that the whole Phanerozoic is strongly influenced by a single record of varying

fossil preservation, including intervals of greater or fewer gaps, so that when the record is bad, all groups react by showing range truncations and thus high extinction values. This is indeed possible and may explain some of the highs and lows in the profiles, but it does not seem credible as a general explanation because of the tremendous variation in biofacies and lithofacies contained in the data.

*Stratigraphic boundaries as attractants of extinctions.*—Synoptic studies of extinction are always plagued by the unfortunate fact that paleontologists are often reluctant to carry taxa over major boundaries, preferring instead to erect new names. Thus, boundaries tend to accumulate extinctions. This is indeed a serious problem and one not amenable to rigorous analysis because it is based on a long history of subjective decisions. The problem

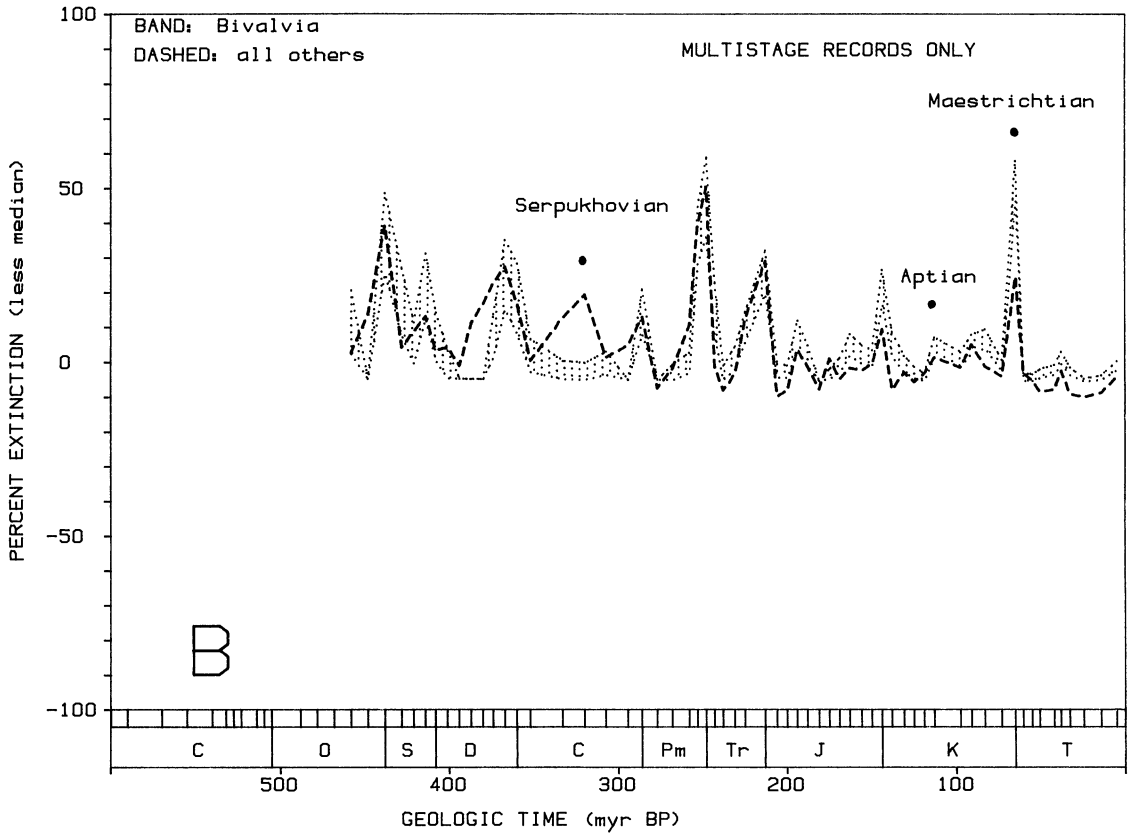


FIGURE 3. Continued.

is troubling in the present context because all fossil groups are prone to the bias.

It is not clear whether this factor is significant or not, but some exploration is possible. One point is clear: the subjective element may enhance an existing extinction peak, but is unlikely to create one. The well-established extinction events—like most of those that mark the system, series, and many stage boundaries—are surely real, for they are clearly marked by the disappearance of distinctive groups of fossils. The most reasonable operational conclusion is to treat the heights of extinction peaks with great caution but to accept their positions in time as not being significantly influenced by artifacts of taxonomic judgment.

In summary, the four alternative explanations for the similarity of extinction profiles are plausible at some scale, but the most likely

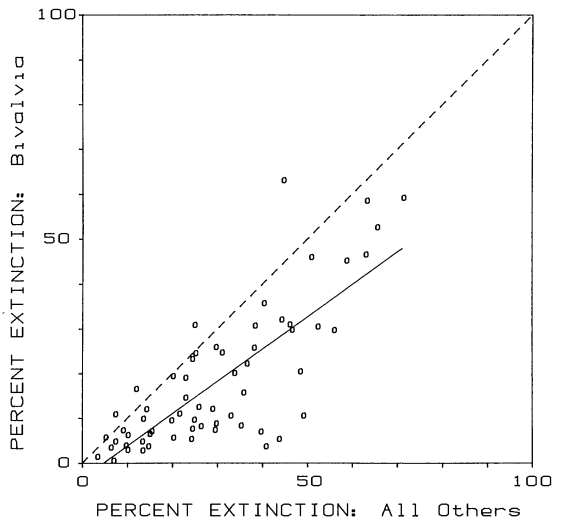


FIGURE 4. Percent extinction per stage for bivalves compared with all other genera (full sample). Bivalves have generally lower volatility than other genera, as indicated by the fact that the points fall mostly below a 45 degree line. Nevertheless, the extinction values for bivalves are highly correlated with those in the total sample.

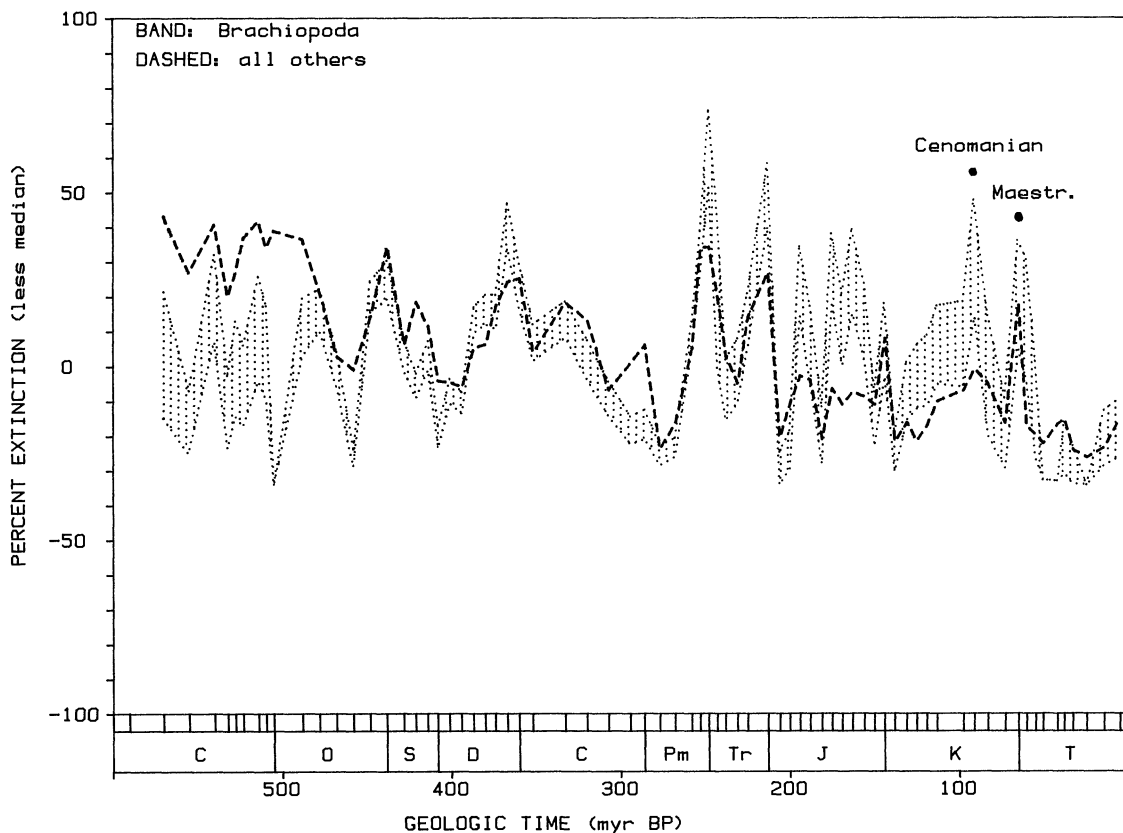


FIGURE 5. Brachiopod extinction compared with that for all other genera. Plotting procedure is that of Fig. 3A.

explanation remains the simplest: that order and class level groups do have remarkably similar generic extinction histories in the Phanerozoic.

#### A Further Test: Reef Faunas

Are significantly different extinction profiles obtained if constructed from samples designed for ecological homogeneity? That is, if we use samples of the Sepkoski data base that cut across taxonomic but not ecological lines, is the signal different? This was tested with a specially collected sample of reef organisms.

Several summaries of the biofacies associated with organic reefs were searched for names of genera common in fossil reef deposits (including the classic wave-resistant structures as well as prominent organic mounds and buildups in shallow marine carbonate facies). A list of references used for

the survey is given in a separate bibliography at the end of this paper.

This survey yielded a list of about 800 genera distributed throughout the post-Cambrian Phanerozoic. It included many obligate reef dwellers, such as frame-building corals, as well as other organisms commonly found on reefs but not necessarily limited to reefs, such as some of the thick-shelled bivalves and gastropods, certain crinoids, trilobites, and so on. Therefore, the list was strongly representative of a single environment limited to shallow marine areas of the tropics and subtropics. The taxonomic composition varied greatly through the Phanerozoic, as one set of frame-building organisms replaced another in the evolution of this adaptive zone (for review, see Sheehan 1985).

The 800 genera from the reef literature were then compared with the Sepkoski data base to identify those with stage-level (or better)

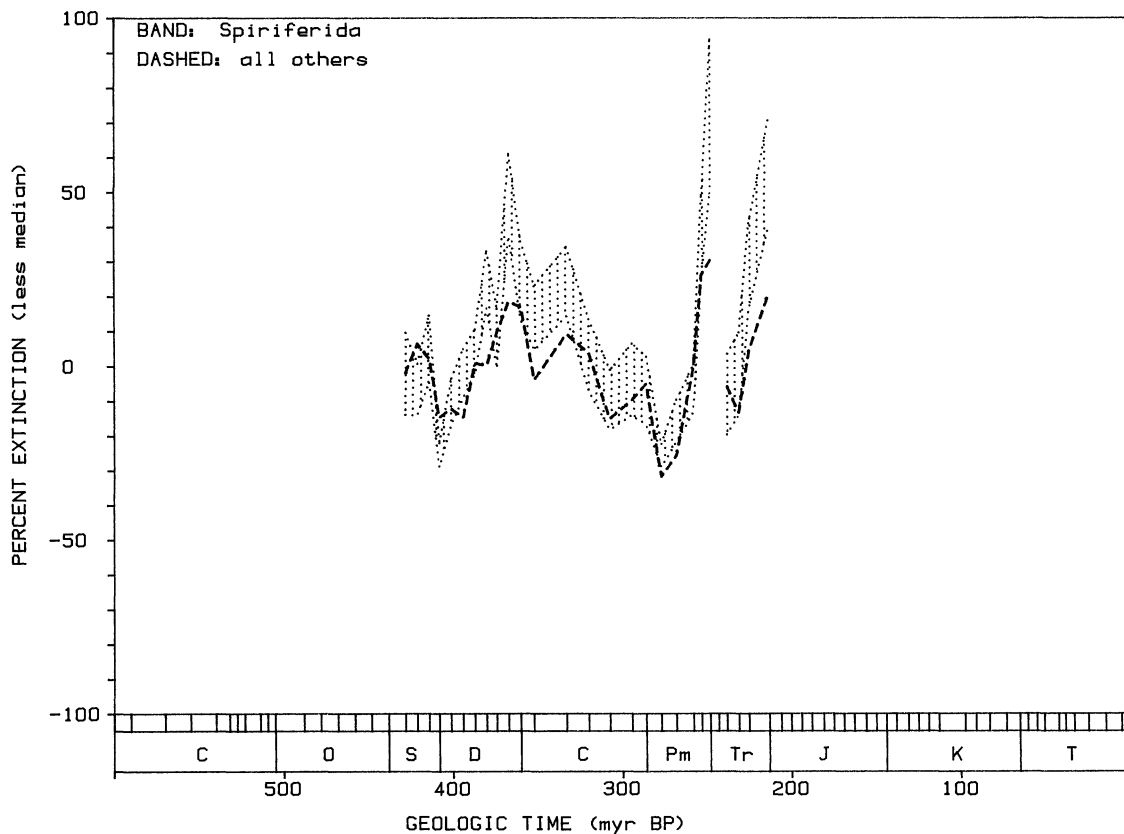


FIGURE 6. Extinction profile for the brachiopod order *Spiriferida* compared with that for all other genera. Plotting procedure is that of Fig. 3A.

stratigraphic ranges. This yielded a residue of 476 genera. Somewhat surprisingly, the stage-by-stage extinction intensities for the reef sample correlate well with those of all other genera. The correlation coefficient ( $r$ ), computed as in Fig. 4, is 0.78, and the extinction profiles are at least as similar as for bivalves and "all other" genera (Fig. 3).

Figure 9 shows the extinction profile for reef invertebrates compared with all other genera. The mode of plotting differs slightly from previous plots (except Fig. 3B) in that only multistage genera were used. This was done because the reef sample is dominated by long-ranging genera (417/476); the review papers that produced the list emphasized common, often ubiquitous fossils. The correlation for this version of the reef sample is very high ( $r = 0.88$ ).

The similarity of the profiles in Fig. 9 is striking, with an almost perfect match be-

tween the reef group and all other genera. The peaks and troughs are all in the same positions and differences in peak height, although present, are relatively minor.

The experiment with the reef sample argues strongly that the similarity of extinction profiles through the Phanerozoic invertebrate record is real and not an artifact of preservational or other biases. But it raises other problems and questions that will be explored, but not resolved, in the following discussion.

### Discussion

If we accept that taxonomic as well as ecological groupings of Phanerozoic genera give approximately the same extinction profiles, what does this tell us about the extinction phenomenon? If extinctions were due mainly to the vagaries of the adaptive success or failure of individual groups or to species interactions, then the record should contain many

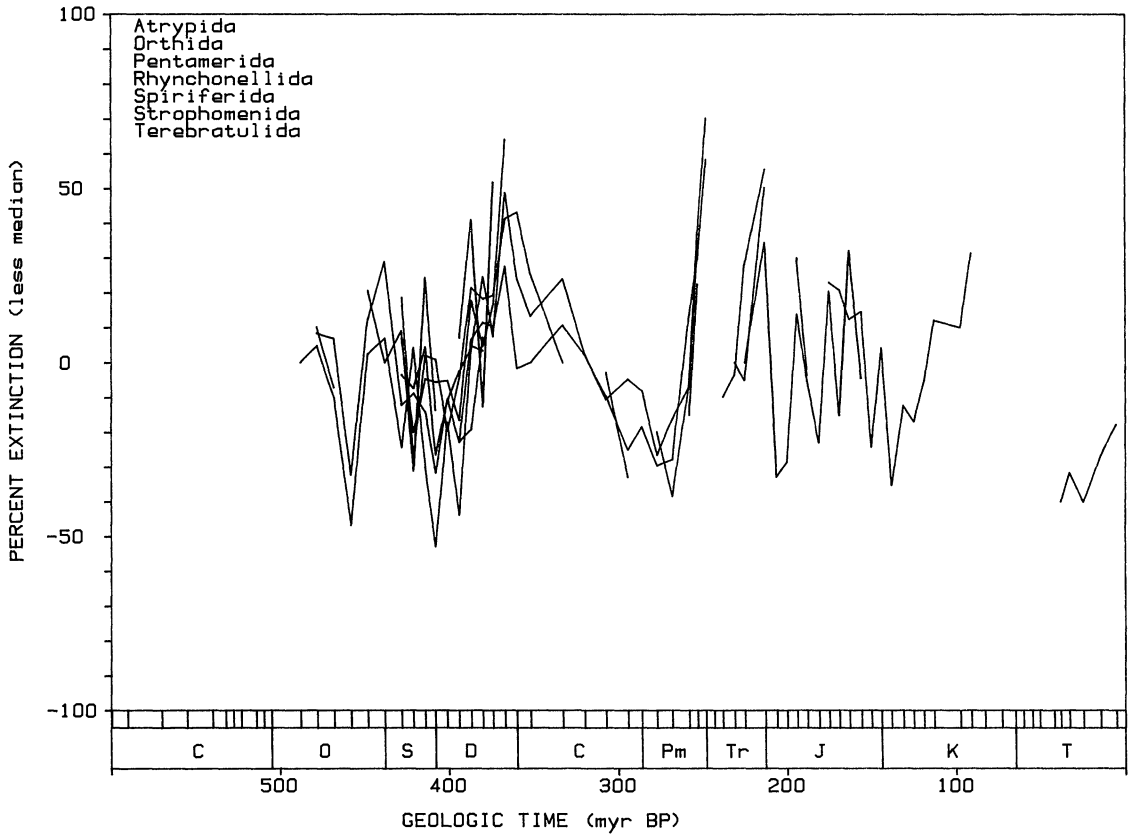


FIGURE 7. Extinction profiles for seven brachiopod orders. Only stages with at least ten genera in an order are plotted.

different extinction histories. But instead, we have extinction events that cut across functional, physiological, and ecological lines, and this suggests common external causes. In other words, the results suggest that extinction is physically rather than biologically driven. When faced with much the same empirical result 35 years ago, Newell (1952) concluded that it "indicates a common external cause" (p. 385). Newell urged sea level change as the principal common cause:

"Great subsidence in mean sea level is regarded here as the most probable cause of concurrent mass extinctions in numerous unrelated orders and classes." (1952: p. 385)

We now have a plethora of candidates for the external causes, including climatic change (Stanley 1987) and collisions with extrater-

restrial bodies (Alvarez et al. 1980). There is no reason that all extinction events must be caused by only one of these. Regardless of mechanism, however, the data suggest strongly that major pulses of extinction (not limited to the biggest mass extinctions) result from geographically pervasive environmental disturbances. The disturbances need not be global in extent. Hallam (1986) has shown, for example, that two well-established extinction pulses, those in the Pliensbachian and the Tithonian, were not global. An environmental perturbation limited to a region or hemisphere may influence global data if the perturbation is sufficiently severe.

But what of the occasional striking departures from the similarity of extinction profiles? Although these are minor elements in the total picture, they may ultimately be the most useful in deciphering the proximal caus-

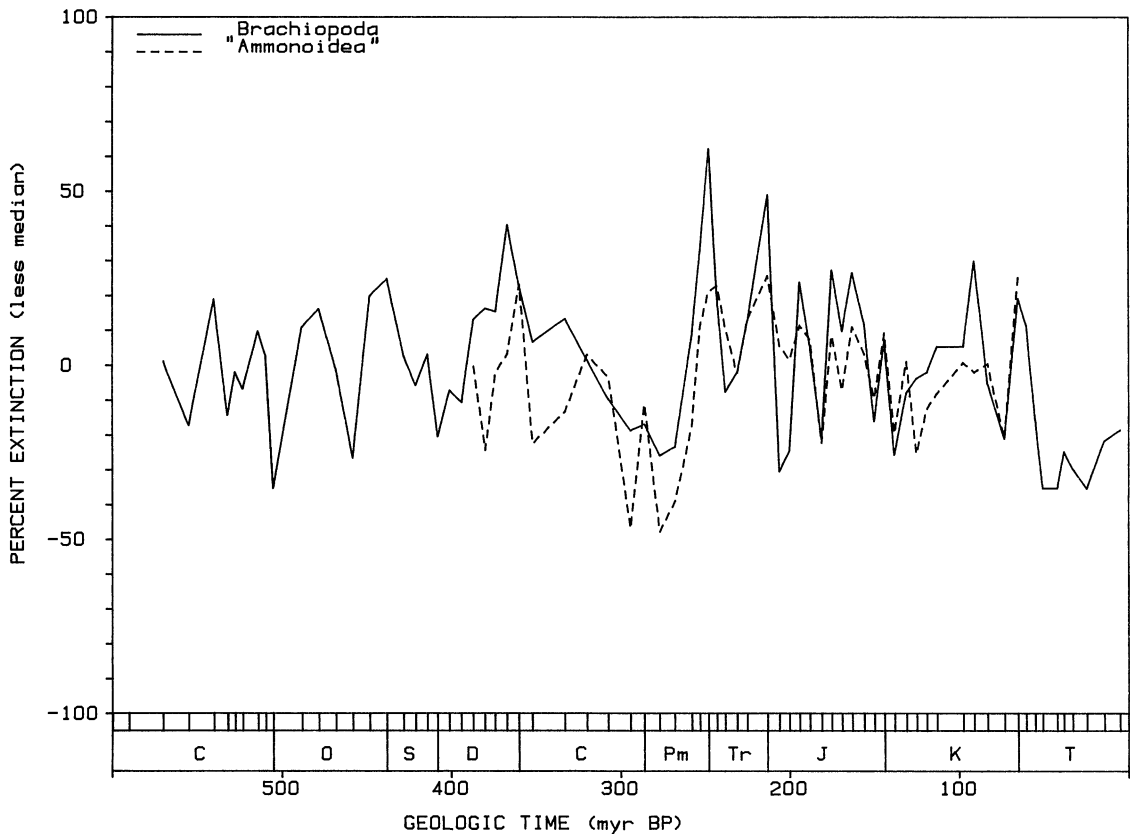


FIGURE 8. Extinction profiles of brachiopods and "ammonoids." See Table 1 for list of orders used for the ammonoid sample.

es of extinction. To this end, we need comprehensive and carefully documented compilations of data which are ecologically, physiologically, or biogeographically based.

An unresolved question coming out of the present analysis is why the suite of reef organisms shows a better match to the total sample of "all others" (Fig. 9) than is seen when individual, large taxonomic groups are plotted (Figs. 3 and 5). At the very least, this provides striking confirmation of Sheehan's conclusion that Phanerozoic reef organisms "... had a pattern of evolution very similar to other marine communities ... ." (Sheehan 1985: p. 46). Reef organisms and the other marine biota were clearly "marching to the same drummer."

Can this interpretation be extended? It is commonly perceived that reefs are affected more severely at major extinction events than

other habitats (see discussion by Jablonski 1986b). If this effect were pronounced, one should expect the extinction peaks for reef organisms in Fig. 9 to be higher than for the "all others" sample, but this is not the case. The lack of difference may mean only that the resolving power of the present data base is insufficient to see a subtle but real effect. The question could be approached by developing new samples of (a) non-reef tropical genera and (b) high latitude genera and comparing these with the reef sample in the format of Fig. 9.

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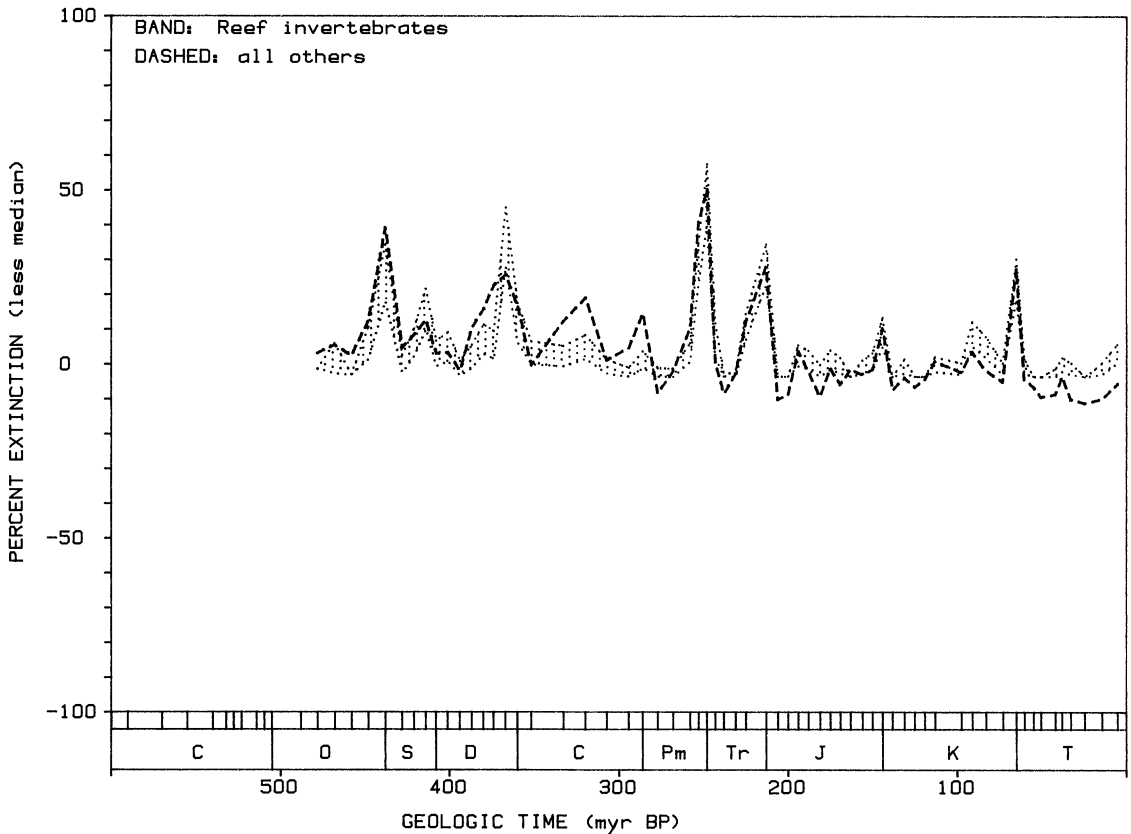


FIGURE 9. Extinction profile for 417 reef genera compared with all other genera. Multistage records only.

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