

A factor analytic description of the Phanerozoic marine fossil record¹

J. John Sepkoski, Jr.

Abstract.—Data on numbers of marine families within 91 metazoan classes known from the Phanerozoic fossil record are analyzed. The distribution of the 2800 fossil families among the classes is very uneven, with most belonging to a small minority of classes. Similarly, the stratigraphic distribution of the classes is very uneven, with most first appearing early in the Paleozoic and with many of the smaller classes becoming extinct before the end of that era. However, despite this unevenness, a *Q*-mode factor analysis indicates that the structure of these data is rather simple. Only three factors are needed to account for more than 90% of the data. These factors are interpreted as reflecting the three great “evolutionary faunas” of the Phanerozoic marine record: a trilobite-dominated Cambrian fauna, a brachiopod-dominated later Paleozoic fauna, and a mollusc-dominated Mesozoic-Cenozoic, or “modern,” fauna. Lesser factors relate to slow taxonomic turnover within the major faunas through time and to unique aspects of particular taxa and times.

Each of the three major faunas seems to have its own characteristic diversity so that its expansion or contraction appears as being intimately associated with a particular phase in the history of total marine diversity. The Cambrian fauna expands rapidly during the Early Cambrian radiations and maintains dominance during the Middle to Late Cambrian “equilibrium.” The Paleozoic fauna then ascends to dominance during the Ordovician radiations, which increase diversity dramatically; this new fauna then maintains dominance throughout the long interval of apparent equilibrium that lasts until the end of the Paleozoic Era. The modern fauna, which slowly increases in importance during the Paleozoic Era, quickly rises to dominance with the Late Permian extinctions and maintains that status during the general rise in diversity to the apparent maximum in the Neogene. The increase in diversity associated with the expansion of each new fauna appears to coincide with an approximately exponential decline of the previously dominant fauna, suggesting possible displacement of each evolutionary fauna by its successor.

J. John Sepkoski, Jr. Department of the Geophysical Sciences, University of Chicago, 5734 S. Ellis Ave., Chicago, Illinois 60637

Accepted: October 24, 1980

Introduction

The fossil record is an extremely complex, multi-component system. When its components are examined individually or in small groups, the complexity of their form, function, interaction, and history often seems overwhelming, and almost infinite, making rigorous generalizations nearly impossible to construct. But sometimes it is possible to assemble the elementary components of a complex system into small subsystems and collect these subsystems into larger subsystems, etc., permitting the entire system to be studied hierarchically. Valentine (1968, 1973) has emphasized this point with respect to paleoecological systems, which he argues can be assembled into hierarchies of spatially more ex-

pansive subsystems, involving individuals, populations, communities, and provinces; the structure and properties of paleoecological systems can then be investigated at any particular level more or less independently, and valid generalizations appropriate to each level can be formulated. More recently, Eldredge and Cracraft (1980) and Gould (1980) have argued that evolutionary (or phylogenetic) systems also are hierarchical and can be studied at the populational level, species level, or transpecific (“macroevolutionary”) level; again, valid generalizations about processes and properties at any particular level can be made without requiring complete knowledge of analogous processes and properties at other levels.

The history of the earth’s biota also may be amenable to hierarchical study. It may be possible in various situations to collect historical entities together into subsystems and then trace

¹ This paper is dedicated to Bernhard Kummel, who taught me the importance of accurate stratigraphy to the study of the history of life.

and even explain the general behavior of these subsystems through time without necessarily understanding the behavior of the individual entities. In this paper I present an analysis that suggests that at least some aspects of the history of changing faunas in the world's oceans can be treated and perhaps best understood within a hierarchical framework. More specifically, I present results of a statistical analysis of data on the diversity of marine families as seen in the fossil record which indicate that

- 1) the major changes in faunal composition that are observed in the marine fossil record through Phanerozoic time are really rather simple and can be decomposed into a succession of a few major "evolutionary faunas," within each of which are long-term changes caused by slow, "background" rates of taxonomic turnover as well as smaller, less regular changes associated with unique aspects of the taxa and times;
- 2) the major evolutionary faunas are each associated with a different level of taxonomic diversity, so that major changes in faunal composition and faunal diversity seem to be aspects of a single historical process.

These conclusions are based upon a factor analysis of data on the number of marine families within metazoan classes from the Cambrian through the Tertiary. The analysis is similar to that performed by Flessa and Imbrie (1973), but the results differ somewhat because of a different treatment and a different data base with enhanced taxonomic and stratigraphic resolution. In the text below, I first describe several aspects of the marine fossil record reflected in this data base and then, after discussing methodology, present results on the "major themes" and "variations upon themes" in the faunal composition of the Phanerozoic marine record. Finally, I discuss how these results relate to the history of taxonomic diversity and the extent to which they are dependent upon taxonomic resolution.

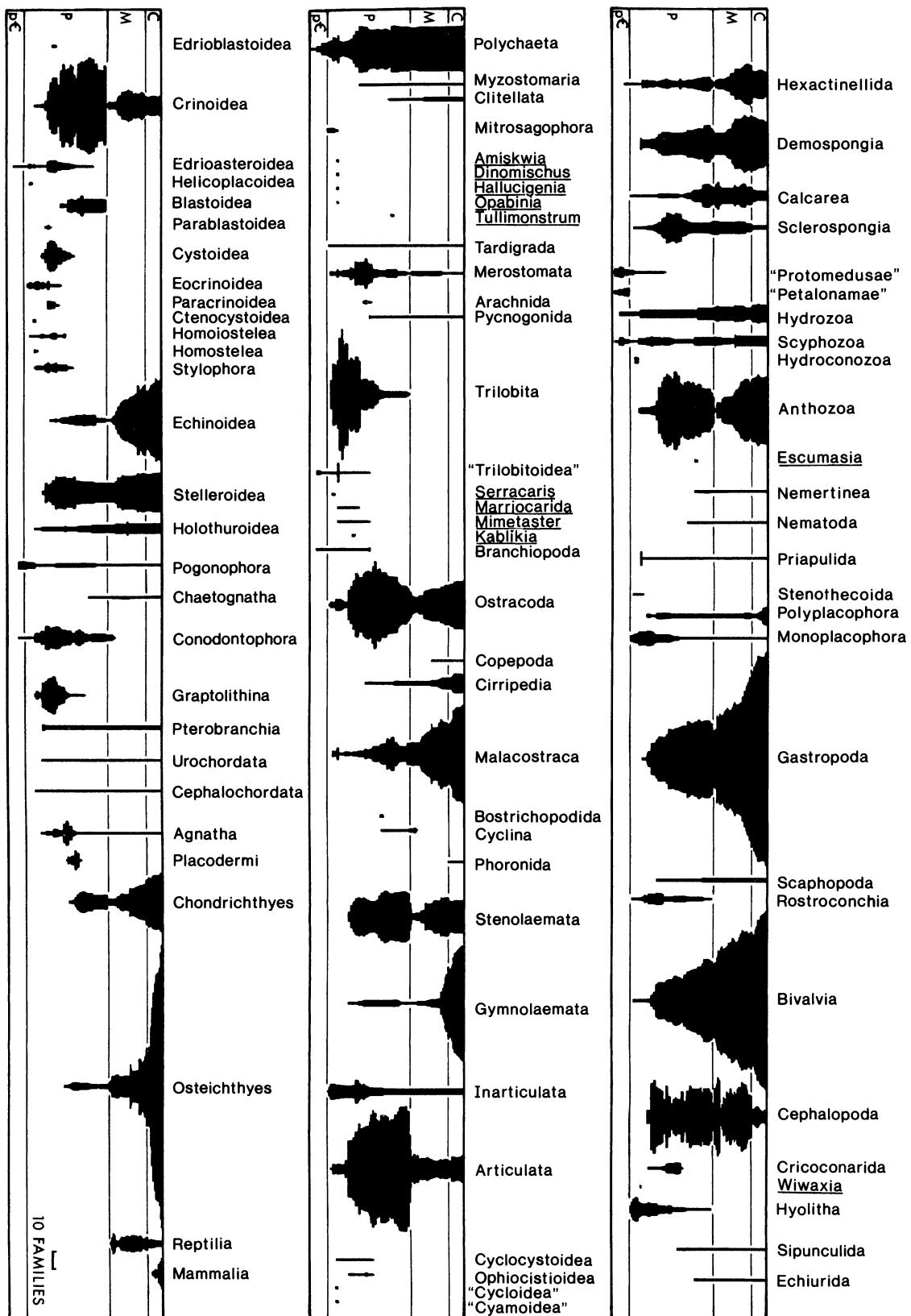
The Marine Fossil Record

Figure 1 displays the marine fossil record (or at least our knowledge of it) in the form of clade, or "spindle," diagrams showing the distribution of families among metazoan classes through the

last 650 Myr of geologic time. Approximately 2800 marine fossil families and 91 classes and class-level *incertae sedis* are represented. These are distributed over 82 stratigraphic stages, providing an average resolution of approximately 8 Myr on the familial diversity of the classes. Absolute time is represented in the vertical dimension, with late Precambrian (mid-Vendian) at the bottom and Pleistocene at the top of each strip.

Perhaps the most striking characteristic of the ensemble of clades is the general unevenness of size, duration, and point of origin. The number of known fossil families within each class is highly skewed, as is generally characteristic of the distribution of subtaxa within higher taxonomic units (see Anderson 1974; Sepkoski 1978). More than half of the classes in Fig. 1 contain fewer than seven fossil families. In contrast, more than half of the families are contained within the seven largest classes. These classes, in descending order, are the Cephalopoda, Articulata (Brachiopoda), Crinoidea, Osteichthyes, Gastropoda, Bivalvia, and Trilobita. An additional 25% of known fossil families are distributed among the next nine largest classes: the Anthozoa, Malacostraca, Ostracoda, Echinoidea, Gymnolaemata, Stenolaemata, Demospongia, Stelleroidea, and Chondrichthyes. Thus, most of the marine fossil record is contributed by just a small handful of animal groups.

The times of first appearance of the classes also is highly skewed, reflecting the early origin of most major groups of animals. Nearly two-thirds (63%) of the classes make their appearances in the first quarter of the illustrated time (i.e. Vendian and Cambrian), whereas only 4% first appear in the last half (i.e. Permian to Pleistocene) (cf. Simpson 1953, 1960; Valentine 1969, 1977). Many of the clades that originate early in the Paleozoic Era remain small and become extinct prior to the end of that era, while those that expand to substantial widths mostly persist to the present (cf. Anderson and Anderson 1975; Gould et al. 1977; Raup 1978a). This pattern makes the Paleozoic Era appear as the "age of small clades" and the Mesozoic and Cenozoic Eras as the age of grand-old, established clades. Of course, there are many exceptions to this generalization. Most noticeable is the Tri-



lobita which expands more rapidly than any other class during the Cambrian Period but then contracts and becomes extinct by the end of the Paleozoic Era. At the other extreme are a variety of very thin clades that appear early in the Phanerozoic and then persist to the present without ever gaining any appreciable diversity. Most of these long, narrow clades, however, represent soft-bodied animals whose fossil records are known from only one or a few occurrences, as, for example, the Nemertina, Nematoidea, Priapulida, Sipunculida, and Echiurida (see Conway Morris 1977). In fact, approximately 20% of the clades illustrated in Fig. 1 owe their existences in the known fossil record to only three deposits: the Burgess Shale, the Hunsrück Shale, and the Mazon Creek concretions. However, these three fossil deposits together are responsible for less than 2% of known fossil families.

Simple statistical generalizations, like these, are fairly easy to make by means of visual examination of the pictographs in Fig. 1. Rigorous historical generalizations, concerning variations in the shapes of clades through time, are more difficult, as noted by Gould et al. (1977). Upon casual circumspection, each clade appears to have its own pattern of variation which it shares with no other clade; and even limited patterns of co-variation seen among scattered clades in restricted intervals of time seem to be contradicted by other clades in other parts of the geologic record. For example, although most classes expand during the Paleozoic Era the tempo and mode of expansion are extremely variable. Some large groups, such as the Cri-

noidea, diversify considerably, while others, such as the Osteichthyes, diversify only a little. Some groups, following their appearances, expand almost continuously throughout the Paleozoic, as seen in the Gastropoda, Bivalvia, and Articulata, others expand to some point and then maintain an almost constant diversity, as seen in the Cephalopoda and perhaps Polychaeeta (see Vermeij 1977); still others expand to a maximum and then contract until the end of the Paleozoic, as seen in the Anthozoa, Ostracoda, and Stelleroidea.

One of the most noticeable historical features in Fig. 1 is the marked contraction of classes associated with the Late Permian extinctions at the end of the Paleozoic Era. This great extinction event is seen as the "waist" in many of the clade diagrams. But even at this very critical point in history, the variation among clades remains considerable (cf. Rhodes 1967). Only four of the 91 classes actually become extinct during the Late Permian, and of these, only the Blastioidea is abruptly truncated (although see Kier 1973); the other three classes, the Rostroconchia, Hyolitha, and Trilobita, all had been waning for some time prior to their Permian demise (cf. Newell 1952). Among the groups that survive the Permian extinctions, responses to the event are quite variable. Some groups, particularly the Articulata and Crinoidea, contract markedly and never again regain their former importance. Other groups, including the Anthozoa and Cephalopoda, also contract markedly but then re-expand to their former sizes. Still others, such as the Demospongia and Gastropoda, show only moderate responses to the ex-

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FIGURE 1. Clade diagrams showing the variation in numbers of marine families within metazoan classes and class-level *incertae sedis* during the last 650 Myr of geologic time. The width of each clade diagram indicates the number of fossil families known from direct fossil evidence or by range extension to have been present in the class during the particular stratigraphic interval. The scale for clade widths is indicated in the lower righthand corner of the figure. Eighty-two stage-level stratigraphic intervals are represented in the vertical dimension, which is scaled to absolute time. In each strip, mid Vendian (late Precambrian) is at the bottom and Pleistocene is at the top; the late Precambrian ("pC"), Paleozoic ("P"), Mesozoic ("M"), and Cenozoic ("C") Eras are labelled at the left ends of the strips.

Data on classification and stratigraphic ranges were compiled from a variety of sources. Principal among these are Harland et al. (1967), Moore and Teichert (1953–1979), and Romer (1966), but these were augmented and updated with some 300 additional literature sources (for further documentation, see Appendix I in Sepkoski 1979). Note that the Recent interval of geologic time is not included in the figure so that classes without known fossil records (e.g., Turbellaria, Trematoda, and Cestoda) do not appear. Also note that only marine families are included so that apparent extinctions of some classes (e.g. Arachnida and Branchiopoda) may only represent their disappearance from the *marine* fossil record. The clade diagrams undoubtedly contain many errors, omissions, and questionable interpretations (particularly pertaining to *incertae sedis*); these, however, should not detract from the overall patterns of growth and decay of the well-established, well-preserved classes that constitute the great bulk of the fossil record.

tinction event, while finally a few large groups, notably the Bivalvia, Malacostraca, and Steleroidea, show virtually no response, at least at the level of family (although see Nakazawa and Runnegar 1973).

The Mesozoic and Cenozoic Eras comprise a 200 Myr interval of expansion for many of the groups that survived the Permian extinctions. Spectacular evolutionary radiations are seen in the Gastropoda, Bivalvia, and Osteichthyes and, to a slightly lesser extent, in the Malacostraca, Gymnolaemata, and Echinoidea. Little real contrast is evident in the shape and distribution of the class-level clades between the Mesozoic and Cenozoic. At most, a slight differentiation can be made between the large groups that radiate throughout the post-Paleozoic interval, including the classes listed immediately above, and those groups that radiate in the Mesozoic and "stabilize" in the Cenozoic, such as the sponge classes and the Anthozoa, Stenolaemata, and, perhaps, Stelleroidea. The only major exception to this overall pattern of post-Paleozoic radiation might involve the Cephalopoda. This class contracts markedly at the end of the Mesozoic, reflecting the extinction of the ammonites. However, the lasting effects of this contraction may be more apparent than real and may simply reflect the ascendency of the predominantly soft-bodied coleoids over the shelled nautiloids and ammonoids; today, there are approximately 33 families of cephalopods in the oceans (Van Valen 1973), which is about equal to the average familial diversity of the class during both the Paleozoic and the Mesozoic Eras.

Historical generalizations beyond this scanty qualitative summary become more difficult to make. Questions concerning how much temporal covariation actually exists among the various classes and how important variations within specific geologic periods are relative to overall patterns of expansion or contraction are best approached with statistical analysis. Multivariate techniques, especially factor analysis, are particularly appropriate since they are capable of reducing the seemingly disparate variation among the numerous clades to a few "composite clades" and of measuring how well these composite clades describe the data at hand. In the remaining sections of this paper, I shall use factor analysis to analyze the data in Fig. 1; from

the results, I shall argue that the major patterns of Phanerozoic evolution in the oceans can be described in terms of just a few great evolutionary faunas that succeed one another in time.

Methodology

Factor analysis is a widely used multivariate statistical technique for reducing the variation in a data set with many variables and samples to a few composite variables or samples. Flessa and Imbrie (1973), Flessa and Levinton (1975), and Smith (1977) have discussed how factor analysis can be used to investigate faunal patterns in data comparable to those illustrated in Fig. 1. These authors used a form of *Q*-mode factor analysis, developed by Imbrie (1963), which attempts to resolve each sample within a data array into a mixture of some small number of uncorrelated (orthogonal) end members. These end members are the "factors" and can be conceptualized as idealized samples. Each actual sample is related to each factor by a "loading" which is essentially the square root of the proportion of the sample that is contributed by that end member. The compositions of the factors are indicated by "factor scores" which show how the variables relate to the factors. In the context of the present analysis, if each factor is an idealized sample, then the scores are measures of the relative importance or diversity of each taxon within that sample. Flessa and Imbrie (1973) conceptualized taxa that share large positive scores on a single factor as forming a "diversity association"; the loading of a stratigraphic interval onto this factor then indicates the relative importance of that diversity association in determining the faunal composition of the interval.

The actual mechanics of performing a *Q*-mode factor analysis are succinctly described in the geologically oriented textbooks on multivariate statistics by Jöreskog et al. (1976) and Mather (1976) (see also Klovan 1975). The mechanics basically involve computing the eigenvectors of the matrix of cross-products of all normalized samples; then determining how many of these eigenvectors are important by examining the magnitudes of the associated eigenvalues (which can be conceptualized as the averages of the loadings on each factor); and finally rotating the selected eigenvectors to "simple-structure" or

end-member configuration. Rotation is necessary in an analysis like the one presented here because it avoids the nonsense associations that appear on raw eigenvectors. For example, the first eigenvector for the data in Fig. 1 would represent the average fauna of the entire figure and thus would include positive contributions from both trilobites and marine mammals; rotation, however, would segregate these classes onto separate factors, properly reflecting their complete lack of stratigraphic overlap.

Several modifications of the data in Fig. 1 were made prior to analysis. Most important was a manipulation performed to equalize the stratigraphic resolution in the data set. The durations of stratigraphic intervals tend to increase back through time (cf. Cutbill and Funnel 1967), with the average lengths of Mesozoic and Cenozoic stages being under 6 Myr and the average length of Paleozoic stages being just under 10 Myr; this is true even with the inclusion of stage-level subdivisions of the Cambrian (see Sepkoski 1979). If this situation were left unaltered, there would be fewer "samples" per unit time from the Paleozoic, and therefore faunal change per unit of Paleozoic time would receive less weight relative to the Mesozoic and Cenozoic in the statistical analysis. To avoid this problem, the two shortest contiguous stages out of every three in the Mesozoic and Cenozoic were lumped together, reducing the number of post-Paleozoic stratigraphic units from 41 to 27; this increased the average duration to about 9 Myr, which is only slightly shorter than the average Paleozoic stage.

Two other aspects of the analyzed data should be noted. First, data from neither the Recent nor the Vendian were included in the factor analysis. Both of these times represent unusual samples of the marine fauna, the Recent because it is a virtually perfect sample (including 1000 soft-bodied families unknown as fossils) and the Vendian because it is an extremely low-diversity sample of predominantly soft-bodied animals. The unique character of the Vendian fossil record may be due primarily to unique taphonomic processes operating during that interval of time (Sokolov 1976; Sepkoski 1979), making the resultant fossil fauna basically incomparable to later fossil faunas. For this reason, and because of the extremely low

stratigraphic resolution, the Vendian was excluded from the data, making the analytic results applicable only to the Phanerozoic *sensu stricto*. Note that exclusion of the Vendian eliminated one class, the "Petalonamae" (i.e. *Rangaea*, *Charnia*, etc.; see Glaessner 1979), reducing the number of analyzed classes to 90.

A second important aspect of the data is that the archaeocyathids and radiocyathids, which are not included in Fig. 1, also were not used in the main factor analysis. These two extinct groups, which are important only in the Lower Cambrian, traditionally have been classified among the Metazoa (or at least Parazoa). This status, however, has been questioned recently by several workers who have emphasized both differences from true animal groups (e.g. Zhuravleva and Miakova 1972) and similarities to various plant groups (e.g. Öpik 1975; Nitecki and Debrenne 1979); my analysis of diversity patterns in the Cambrian (Sepkoski 1979) also suggests that archaeocyathids had a unique evolutionary history, which is consistent with the idea that these are not metazoans. However, good arguments for the animal-like nature of archaeocyathids remain (e.g., Balsam and Vogel 1973; Vogel 1978), and the question of their affinity is by no means resolved. Thus, I have repeated certain parts of the factor analysis with the five "classes" of archaeocyathids and radiocyathids recognized by Hill (1972) included among the data; the results are noted in the relevant parts of the discussion below. (The Cribrariocyathida, which were discussed along with the archaeocyathids by Hill [1972], were included among the Polychaeta in all analyses, following Glaessner [1976].)

Thus, the primary data array used in the factor analysis consisted of numbers of marine families within 90 metazoan classes. Following the procedure of Flessa and Imbrie (1973) and Smith (1977), the classes were treated as variables that were "sampled" in each of 63 stratigraphic intervals ranging from earliest Cambrian to Plio-Pleistocene. However, in contrast to the previous authors, no attempt was made to equalize the weights of the variables by percent range or any other transformation. This is because I am more interested here in succinctly summarizing the fauna of each interval of time than in searching for associations of taxa that

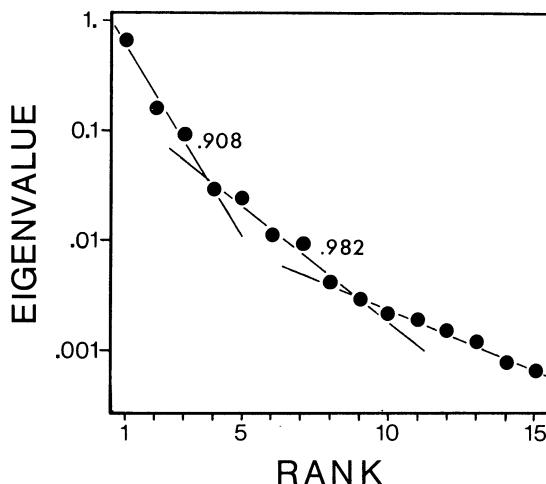


FIGURE 2. A scree graph showing relative eigenvalues from a *Q*-mode factor analysis of families within classes plotted logarithmically against their ranks. In graphs of this type, substantial breaks in the slope of the decay of eigenvalues often reflect changes in the nature of the eigenvectors (i.e. unrotated factors), as, for example, change from factors incorporating systematic variation within the data to factors incorporating observational error. The graph illustrated here is interpreted as showing two major breaks in the decay of eigenvalues, as indicated by the line segments fitted to the groups of points (see text for further discussion). The decimal fractions listed next to the intersections of the line segments are the cumulative proportions of the data accounted for by the eigenvectors to the left of the breaks.

share common times of maximum and minimum diversities. In addition, the avoidance of variable transformations prevents rare, soft-bodied groups present in some intervals "by chance" or by range extension from being assigned more weight in the analysis than is warranted by their scanty fossil records. The result of this treatment of the raw data was that diversities in any "sample" ranged from 0 to 145 families; however, nearly one third of the "variables" had maximum diversities of one, and just over half had maximum diversities of less than five. All diversities were converted to relative diversities within samples by the normalization procedure used in *Q*-mode factor analysis.

All factor analyses were performed with the BMDP4M computer program (Brown 1977). This general-purpose factor analysis program was used instead of the popular CABFAC *Q*-mode vector analysis program, described by Klovan and Imbrie (1971), simply because the version of CABFAC available to me was too small to handle the 90 variables in the data ar-

ray. Rather than modify this program, I "tricked" the BMDP4M program into performing comparable computations by (1) transposing the raw data so that stratigraphic intervals appeared as columns in the input array and (2) instructing the program to compute a "correlation matrix about zero" rather than the column means. The resultant "correlation" matrix thus was actually a cosine θ matrix measuring the pairwise faunal similarities of the stratigraphic intervals. All factors were computed from this matrix. Predetermined numbers of factors were rotated to end-member positions using the VARIMAX procedure in separate runs of BMDP4M.

Factor Analytic Results

Number of factors.—Perhaps the most arbitrary aspect of most factor analyses is determining how many factors are necessary to describe the data adequately. This determination, however, should be done prior to any rotation so that information considered to be trivial or to be due to observational error does not influence the final composition of factors. There are a variety of guidelines for determining just how many factors are important in a given analysis. Most workers select factors that have relatively large eigenvalues which sum to some arbitrarily large value. These two criteria were used here with the additional stipulation that the difference between successive eigenvalues be relatively large. The reason for this is that a *Q*-mode factor analysis of a random number table would produce some eigenvalues that were larger than others but with differences that were rather small; if the eigenvalues were sorted from largest to smallest and plotted logarithmically against their ranks, to produce a "scree graph," the points would fall close to a straight line with a relatively gentle slope. If several sets of systematically correlated variables were added to the random number table and the entire analysis repeated, the scree graph would exhibit an initial rapid decay of eigenvalues associated with the systematic variables, followed by an abrupt break in slope and then a much gentler decay of eigenvalues associated with the statistical "noise" contributed by the random numbers (see Linn 1968).

The scree graph resulting from the factor

analysis of the modified faunal data is illustrated in Fig. 2. The graph suggests an interesting structure underlying the faunal data, with three rather than two distinct sets of factors, as indicated by the interpretive straight lines fitted to the points. If there were only two sets of points, falling along line segments of substantially different slope, it might be possible to interpret the structure of the observed fossil record as consisting of a few systematic components of faunal variation coupled with random observational errors, as in the conceptual model above. However, the three sets of eigenvalues apparent in Fig. 2 actually suggest a more interesting, hierarchical structure to the marine fossil record. The first three factors, which together account for nearly 91% of the data, seem to represent the "three great evolutionary faunas" of the Phanerozoic marine fossil record; these factors, when rotated, receive positive loadings from virtually all stratigraphic intervals, preserve large communalities for all but two intervals, receive few large negative scores from the classes, and remain essentially invariant when more factors are added and rotated. The next set of four factors accounts for an additional 7.5% of the data and can be considered as reflecting secondary temporal variations or contrasts within the major evolutionary faunas; factors within this set display both positive and negative loadings which, with only one exception, are always smaller than the maximum loadings on the first three factors for any given stratigraphic interval. The final set of factors in Fig. 2 probably encompasses both "observational error" and minor faunal variations that involve a few families within a few adjacent stratigraphic intervals; no factor in this set accounts for more than 0.3% of the total fauna data or more than 5% of the faunal composition of any single stratigraphic interval.

Factors I through III: The three great marine faunas of the Phanerozoic.—Loadings of stratigraphic intervals on the first three rotated factors are plotted against absolute time in Fig. 3. Note that the factors have been reordered into temporal sequence and renumbered with Roman numerals. The importance of each rotated factor is indicated by the relative eigenvalue (λ) given at the bottom of the figure. Factor scores, representing the taxonomic composition of the

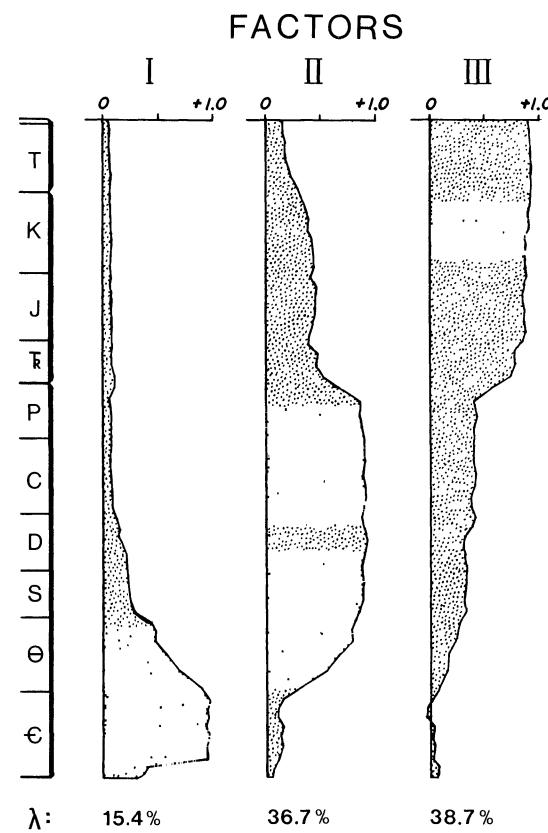


FIGURE 3. Loadings of stratigraphic intervals on rotated factors from a three-factor *Q*-mode analysis of families within classes, plotted against absolute time (vertical scale). Geologic systems are indicated by the abbreviations in the bar at the left, and relative eigenvalues (λ 's) are listed for each factor at the bottom. The three factors are interpreted as representing the three "great evolutionary faunas" of the Phanerozoic marine fossil record; thus, the loadings on the factors reflect the waxing and waning of the faunas through time. Note that all loadings are positive, except for two very small loadings on Factor III, and that each factor has dominant and nearly invariant loadings over a relatively discrete interval of geologic time. All stratigraphic intervals, except the Tommotian, preserve high communalities in this three-factor solution.

three factors, are summarized in Table 1. Note that very few classes have large negative scores on any given factor and that those which do are the classes most important on other factors, as, for example, the Articulata, Crinoidea, and Trilobita on Factor III. These negative scores are somewhat difficult to interpret but seem to reflect, basically, the conspicuous absence of a diverse class and/or a decline in that class when the fauna represented by the particular factor is expanding (or vice versa). The negative scores originate from the somewhat arbitrary mathe-

TABLE 1. Summary of scores of taxonomic classes on the first three rotated factors. All classes with scores greater than 0.05 or less than -0.05 are listed in descending order of magnitude on each factor. Minor classes with scores that do not exceed 0.05 generally have their maximum scores on the factor that is most important over the stratigraphic intervals in which the classes reach their peak familial diversities or spend the greatest part of their durations. Percentages in parentheses indicate the cumulative proportion of each factor contributed by the classes listed to that point.

Scores	FACTORS		
	I	II	III
>0.5	Trilobita (77%)	Articulata (39%)	Gastropoda Bivalvia (58%)
>0.2	"Polychaeta" (83%)	Crinoidea Ostracoda Cephalopoda Anthozoa (86%)	Osteichthyes Malacostraca Echinoidea (83%)
>0.1	Monoplacophora Inarticulata Hyolitha (93%)	Stenolaemata Gastropoda Stelleroidea Bivalvia (92%)	Gymnolaemata Demospongia Chondrichthyes Polychaeta Hexactinellida Stelleroidea (93%)
>0.05	Conodontophora Graptolithina Pogonophora Eocrinoidea Merostomata Scyphozoa Malacostraca (97%)	Demospongia Conodontophora Merostomata Blastoidea Graptolithina Polychaeta Sclerospongia Cystoidea (96%)	Cephalopoda Calcarea Anthozoa Hydrozoa Reptilia Stenolaemata (96%)
<-0.05	Crinoidea	Gymnolaemata Echinoidea	Trilobita Crinoidea
<-0.1		Osteichthyes	Articulata

matical constraint that the factors be uncorrelated; this evidently leads to rotated factors being positioned just beyond the realm of the real faunas which comprise the stratigraphic intervals and which, of course, have no negative constituents. Oblique rotation of the factors presumably would avoid this problem. However, judging from the very high maximal loadings of particular stratigraphic intervals on the orthogonal factors, oblique rotation would not substantially alter the loadings; thus, such rotation was not attempted.

The temporal pattern of variation exhibited by the loadings in Fig. 3 suggests that there is a fundamental simplicity to all the faunal change we see in the marine fossil record; this seems true in spite of the almost chaotic variation initially apparent in Fig. 1. Again, over 90% of the clade data can be explained in terms of three "evolutionary faunas," each of which

is dominant for a long interval of time and then is rapidly replaced by another fauna. This pattern of long intervals of approximate stability punctuated by rapid rises and falls of factor loadings seems to be quite different from patterns that can be generated from simple random branching processes. Smith (1977) showed that factor loadings computed for stochastic clades or for evenly distributed, independent clades exhibit bell-shaped patterns of change with respect to time; the loadings on any given factor increase slowly through time, reach a relatively narrow, rounded peak, and then decline slowly again for the remainder of time (see especially Figures 2 and 3 in Smith 1977). Smith argued that this was basically the pattern uncovered by Flessa and Imbrie (1973) and that therefore one cannot conclude that their analysis demonstrated the existence of distinct, temporally coherent "diversity associations." In contrast, the results

presented in Fig. 3 of the present paper differ considerably from the patterns generated by Smith (1977) and therefore suggest that there may be more structure to the marine fossil record than uncovered by Flessa and Imbrie. Still, there are similarities between the two analyses despite substantial differences in data and treatment; the temporal variations in Factors I, II, and III in Fig. 3 correspond approximately to Flessa's and Imbrie's Marine Factors 1, 3, and 7, respectively.

The first factor in Fig. 3 encompasses the Cambrian fauna. As indicated by the scores in Table 1, this factor is dominated by Trilobita with additional important contributions by "Polychaeta" (including cibricyathids, coleolids, and volborthellids; see Glaessner 1976), Monoplacophora, Inarticulata, and Hyolitha, together, these classes constitute nearly 93% of the fauna represented by Factor I. The factor rises very quickly through the two Tommotian intervals (the only intervals not adequately described by the first three factors) and then completely dominates the data for the remainder of the Cambrian Period. After the start of the Ordovician, the factor begins a rapid decline, which continues in an approximately exponential fashion until the late Paleozoic Era; thereafter the factor maintains low loadings representing the persistence of a few families of inarticulate brachiopods, monoplacophorans, pagonophorans, and perhaps several other classes.

The succeeding Paleozoic fauna, which is encompassed by Factor II, is present in low abundance throughout the Cambrian Period but then bursts to dominance with the great radiation of the "shelly fauna" during the Ordovician. Classes that are important on this factor include Articulata, Crinoidea, Ostracoda, Cephalopoda, and Anthozoa and, to a lesser extent, Stenolaemata, Gastropoda, Stelleroidea, and Bivalvia (Table 1); together, these classes constitute a taxonomically more diverse group than the Cambrian fauna. Following its Ordovician rise, Factor II maintains complete dominance for some 200 Myr until the end of the Paleozoic Era. The great extinction event of the Late Permian effects a rapid turnaround in faunas, and Factor II falls to a subdominant position, which it maintains throughout most of the Me-

sozoic Era. The final decline of the Paleozoic fauna appears to begin in the Late Cretaceous and to continue, again in an approximately exponential manner, through the Cenozoic.

Factor III represents the Mesozoic-Cenozoic, or "modern," fauna. During the Cambrian Period this factor has very small positive to negative loadings, none of which probably differs significantly from zero. Factor III first becomes important during the Ordovician Period at the same time that Factor II is rapidly rising. Factor III then increases very slowly through the remainder of the Paleozoic Era but ascends rapidly to dominance at the expense of Factor II during the latest Permian and earliest Triassic. The scores summarized in Table 1 indicate that Factor III is dominated by molluscs, primarily Gastropoda and Bivalvia and, to a much lesser extent, Cephalopoda. Other important groups include Osteichthyes, Malacostraca, Echinoidea, Gymnolaemata, Demospongia and Hexactinellida, Chondrichthyes, Polychaeta, and Stelleroidea. Again, the primary constituents of this factor seem somewhat more diverse than those preceding it. Notice, however, that some of the classes important on Factor III are also important on the other factors. This dual importance may reflect consistently high familial diversities over long intervals of time, as seen, for example, in the Bivalvia, or strongly polymodal diversities, as seen in the Stenolaemata (see also Flessa and Imbrie 1973). In most instances, however, the presence of high scores on more than one factor probably reflects a heterogeneous taxonomic structure underlying the class. For example, high scores of Gastropoda, Anthozoa, and Cephalopoda on Factor III reflect the Mesozoic and Cenozoic importance of meso-, neo-, and opisthobranch gastropods, scleractinian corals, and ammonoid and coleoid cephalopods; these groups are different from the archaeogastropods, rugose and tabulate corals, and nautiloid cephalopods which are responsible for the high scores of the same classes on the Paleozoic Factor II.

Factors IV through VII: Variations upon themes.—If the first three factors can be considered as reflecting the great evolutionary faunas, or fundamental compositional themes, of the Phanerozoic oceans, then the next four factors must be considered variations upon these

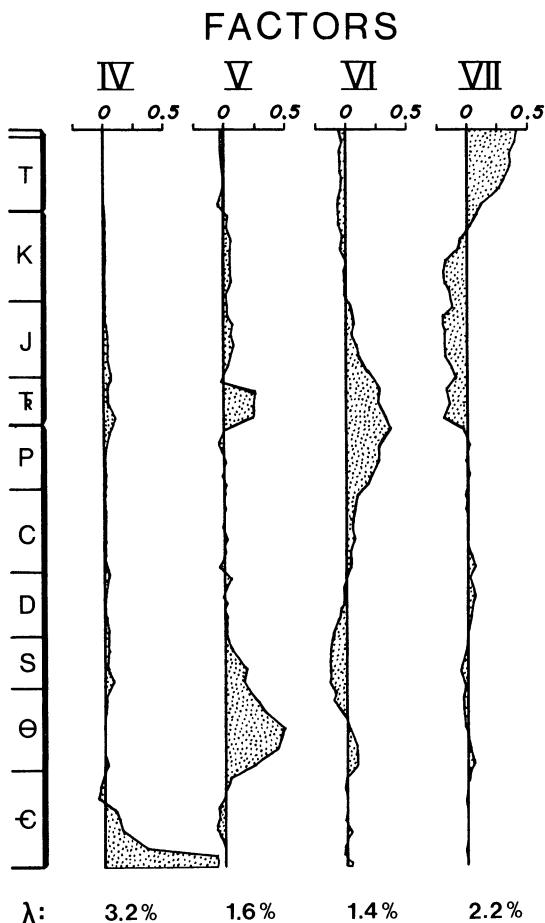


FIGURE 4. Loadings of stratigraphic intervals on rotated Factors IV to VII from a seven-factor *Q*-mode analysis of families within classes, plotted against absolute time. (Factors I to III, which are not shown, are nearly identical to the three factors illustrated in Fig. 3.) Graphing conventions are the same as in Fig. 3. The four factors illustrated here accommodate temporal contrasts of secondary importance within the three great evolutionary faunas; these contrasts are associated with major evolutionary radiations and with low levels of taxonomic turnover through time. Note that nearly all stratigraphic intervals have loadings on Factors IV to VII that are considerably smaller than their maximum loadings on the first three factors. The only exceptions involve the Tommotian Stage of the Cambrian, comprising two stratigraphic intervals in this data set which have their maximum loadings on Factor IV; this exception probably reflects small-sample phenomena, as discussed in the text.

themes. This second set of four factors picks up two kinds of secondary faunal variations:

1. long-term changes in faunal composition caused by normal, or "background," taxonomic turnover within the major evolutionary faunas during the lengthy stretches of the post-Ordovician Paleozoic and the Mesozoic-Cenozoic;

2. shorter-term changes associated with major evolutionary radiations.

Interestingly, much of the residual temporal variation left from the first three factors seems to be concentrated in the intervals of the great evolutionary radiations, specifically the Early Cambrian, Ordovician, Triassic, and Late Cretaceous-Tertiary. Most of this residue is incorporated into Factors IV through VII which, when rotated along with the first three factors, account for 8.5% of the faunal data. It should be noted that this rotation barely changes the loadings and scores on Factors I to III and, in fact, does not leave Factors IV through VII substantially different from the unrotated fourth through seventh principal vectors (i.e., "raw" eigenvectors).

Loadings on rotated Factors IV through VII are graphed against time in Fig. 4; the factors have been reordered and renumbered in the same manner as the factors in Fig. 3. As can be seen by comparison to Fig. 3, only one factor in Fig. 4 dominates the taxonomic composition of any of the 63 stratigraphic intervals. This single factor is Factor IV, which encompasses the pre-trilobite Tommotian fauna of the earliest part of the Cambrian Period. From the partial list of scores in Table 2 it can be seen that this fauna includes many of the classes important in Cambrian Factor I, such as "Polychaeta," Pogonophora, Hyolitha, and Monoplacophora, but excludes Trilobita, as indicated by the large negative score of that class on Factor IV. Archaeocyathids fall almost exclusively onto this factor when they are included in the analysis; their addition increases the proportion of data incorporated into Factor IV from 3.2% to 5.8% and extends the range of the factor's dominance up to the Botomian Stage of the Lower Cambrian.

The apparent importance of Factor IV, both with and without archaeocyathids, probably reflects the statistics of small samples more than any broad patterns of evolutionary interest. Consider a large urn filled with balls of many colors. If we begin drawing balls at random from the urn, the color composition of our sample initially will be unstable and will fluctuate markedly as the first few balls are drawn; only as the sample becomes large will the composi-

TABLE 2. Summary of scores of taxonomic classes on rotated Factors IV to VII. Conventions are the same as in Table 1 except that cumulative percentages are not listed.

Scores	FACTORS			
	IV	V	VI	VII
>0.5	"Polychaeta"	Cephalopoda		Osteichthyes
>0.2	Pogonophora Hyolitha Monoplacophora Mitrosagophora Protomedusae	Graptolithina Cystoidea Conodontophora	Articulata Bivalvia	Gymnolaemata Articulata
>0.1	Inarticulata Edrioasteroidea Branchiopoda Trilobitoidea	Stenolaemata	Cephalopoda Polychaeta Calcarea	
<-0.1		Malacostraca Crinoidea Anthozoa	Graptolithina Cystoidea Stelleroidea	Stelleroidea Demospongia Reptilia Calcarea
<-0.2	Trilobita		Crinoidea Ostracoda Echinoidea Stenolaemata Anthozoa	Cephalopoda Bivalvia

tion stabilize and approach the populational composition of the urn. The same kind of statistical variation seems to be causing the very low-diversity fauna of the earliest Cambrian to appear unique in the factor analysis. This is not to claim that the composition of this fauna is somehow random. Rather, it is simply a statement that the appearance of a new taxon, governed by whatever causes, influences the proportional composition of a low-diversity fauna more than a high-diversity fauna, so that the compositions of faunas can be expected to vary more rapidly during times of low diversity than times of high diversity.

Faunal variation during the second great evolutionary radiation of the Phanerozoic is encompassed by Factor V. This Ordovician radiation factor receives large positive scores from classes that undergo major evolutionary expansions very early in the Ordovician Period; included among these are the Cephalopoda, Graptolithina, Cystoidea, Conodontophora, and Stenolaemata (see Table 2). These groups are contrasted to a set of classes, including the Anthozoa, Crinoidea, and Malacostraca, that extend further back into the Cambrian Period

and take more of the Paleozoic Era to attain their maximum diversities. The relatively high loadings on Factor V in the Triassic, following the Permian extinctions, may be largely accidental, reflecting the rapid rediversification of cephalopods (but ammonoids rather than nautiloids) and the marked constriction of anthozoans and crinoids. The high loadings in the Ordovician and secondary high in the Triassic make Factor V comparable in stratigraphic distribution to Marine Factor 2 of Flessa and Imbrie (1973).

Factor VI, which is comparable to Flessa's and Imbrie's Marine Factor 4, appears primarily to pick up the slow taxonomic turnover that occurs throughout the long post-Ordovician stretch of the Paleozoic Era. This background change translates into a mild contrast in faunal composition between the middle and late Paleozoic, heightened perhaps by the short-term Frasnian-Famennian extinction event (see Boucot 1975). The classes that have large negative scores on Factor VI (Table 2) are those that reach their maximum Paleozoic diversities in the early to middle part of the era and are declining in (or have declined by) the Permian;

these include the Anthozoa, Stenolaemata, Echinoidea, Ostracoda, and Crinoidea (see Fig. 1). These classes are contrasted to several large groups whose greatest post-Ordovician diversities are attained in Permian Period; included most prominently among these are the Articulata, Mollusca (bivalves, cephalopods, and gastropods), Polychaeta, and Calcarea (Porifera). The carryover of Factor VI into the early Mesozoic reflects the relatively high Triassic diversities of most of the latter set of classes (excepting, of course, Articulata) as compared to the reduced diversities and delayed radiations of the first set. The small positive loadings this factor receives low in the Ordovician seems to reflect the rapid radiations of Articulata, Bivalvia, and Cephalopoda in the first half of that period.

The last factor in Fig. 4 finally contrasts the class-level faunas of the Mesozoic and Cenozoic. This factor is similar in stratigraphic distribution and, to a lesser extent, taxonomic composition to Marine Factor 6 of Flessa and Imbrie (1973). The classes that are most influential in affecting the negative loadings on Factor VII over the Mesozoic intervals are the Bivalvia, Cephalopoda, Calcarea and Demospongia, marine Reptilia, and Stelleroidea (Table 2). These large classes, with the exception of Bivalvia, attain familial diversities in the Mesozoic that are greater than or equal to their maximum Cenozoic diversities (see Fig. 1). This is in marked contrast to the Osteichthyes and Gymnolaemata, which undergo particularly massive radiations in the Cenozoic and have large positive scores on Factor VII. Classes with smaller positive scores (i.e. 0.05 to 0.1) include Gastropoda, Chondrichthyes, and marine Mammalia. The large negative score of the Bivalvia and large positive score of the Articulata are somewhat difficult to interpret. Evidently, the inclusion of the Bivalvia among the Mesozoic groups signifies that bivalves constitute a smaller portion of the total modern fauna in the Cenozoic than in the Mesozoic, despite their continuing expansion. The even more anomalous inclusion of the Articulata among the Cenozoic classes probably reflects a strong negative correlation between the Phanerozoic diversities of articulate brachiopods and of several of the Mesozoic groups instead of any im-

portance of brachiopods per se during the Cenozoic Era.

The proportion of the faunal data accounted for by Factor VII is only 2.2%, ranking it fifth in importance among the factors. Thus, the class-level distinction between the faunas of the Mesozoic and Cenozoic Eras appears to be of secondary importance and certainly of less importance than differences between the Paleozoic and Mesozoic Eras or even the Cambrian and Ordovician Periods.

Relationship to Total Diversity

The primary conclusion that can be drawn from the factor analysis is that the faunal change we see in the Phanerozoic marine fossil record is actually rather simple, at least at the level of families within classes. But this should be of no real surprise to any paleontologist who has walked out a variety of stratigraphic sections or has picked through a number of museum drawers. Stratigraphic collections from the Cambrian seem to be dominated by trilobites, whereas those from the later Paleozoic often have numerous articulate brachiopods (or, perhaps, crinoids, nautiloids, and rugose corals); collections from the Mesozoic or Cenozoic, in contrast, usually contain an inordinate number of molluscs (see also Raup 1976). It is gratifying that the computer-based statistical analysis produces results that are consistent with field intuition.

Of course, the factor analysis does more than merely formalize intuition. It also measures the importance of each fauna (and the magnitude of change between faunas; cf. Flessa and Imbrie 1973) and, perhaps more importantly, identifies the full history of each fauna and separates long-term or minor changes within each from the consistent patterns that make it coherent. Thus, for example, the three-factor solution shows that the "modern" fauna has a history that extends with apparently only minor change well back into the Paleozoic and that the modern fauna's rise to dominance occurred very rapidly near the beginning of the Mesozoic.

One very interesting aspect of the history of each major evolutionary fauna is that its rise and decline appear to be intimately related to patterns of total diversity in the Phanerozoic oceans. This can be shown graphically by re-

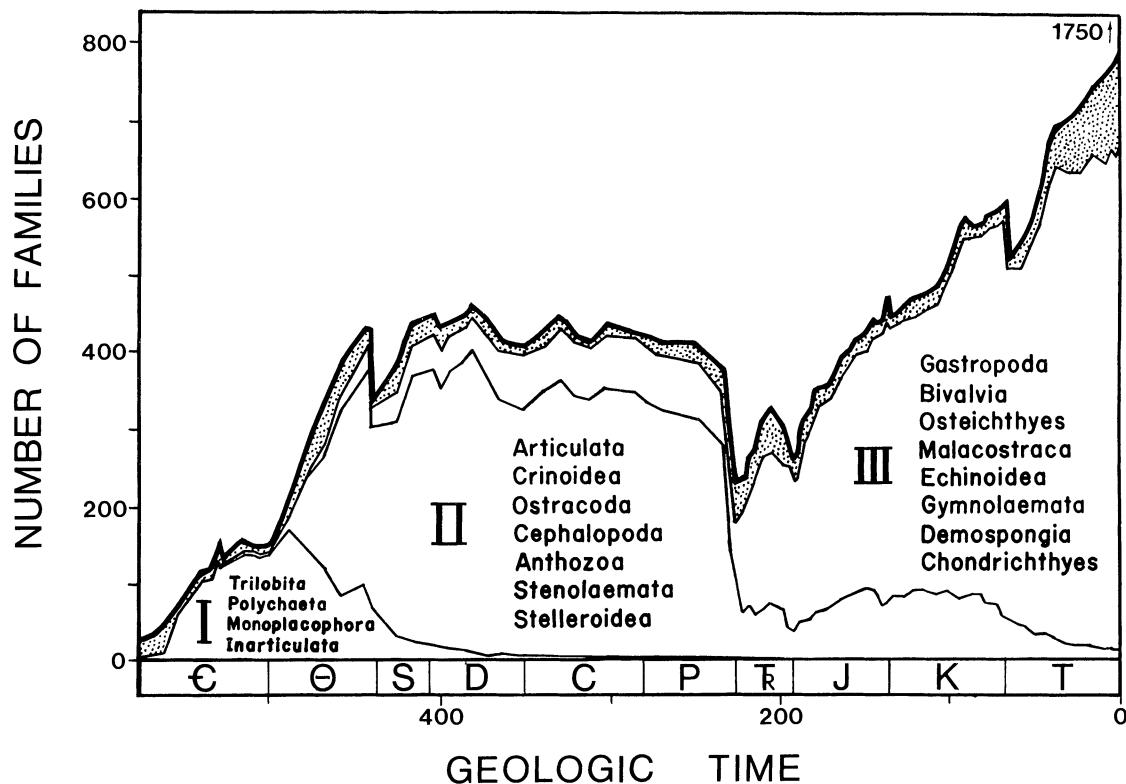


FIGURE 5. Loadings on the first three factors rescaled to total Phanerozoic diversity and depicting the history of the three “evolutionary faunas” as components of total marine diversity. The dark uppermost curve, which shows the total number of metazoan families known from the marine fossil record through geologic time, was obtained by summing all of the clades in Fig. 1. The fields below, which are labelled with Roman numerals corresponding to the factors in Fig. 3, indicate the amount of diversity that can be attributed to each of the factors; taxa listed within each factor are the classes that contribute the greatest amount to (i.e. have the largest scores on) that particular factor (see Table 1). The stippled field immediately below the curve for total diversity represents the residual diversity not accommodated by the three factors.

The number “1750” in the upper lefthand corner is the approximate number of metazoan families that have been described from the modern oceans. More than two-thirds of the nearly 1000 modern families unknown from the fossil record are distributed among the Osteichthyes, gastropods (mostly nudibranchs), malacostracan arthropods, non-scleractinian anthozoans, polychaete, turbellarian, and trematode worms, hydrozoans, and tunicates (listed in order of decreasing importance).

scaling the loadings on the first three factors to total familial diversity, as is illustrated in Fig. 5. The rescaling for this figure was accomplished by first squaring the factor loadings, so that they became proportions of unity, and then simply multiplying each by the total number of families known from each interval of time. Thus, in Fig. 5, the dark uppermost curve represents total familial diversity through the Phanerozoic, obtained by summing all the clade diagrams in Fig. 1. The field labelled “I” is the amount of this diversity accounted for by Cambrian Factor I; the field labelled “II” is that amount accounted for by Paleozoic Factor II; etc. Finally, the stippled field below the upper-

most curve represents the residual diversity that cannot be accounted for by the first three factors alone. Note that, compared to the other fields, the residual field is rather small and uniform, becoming large only in the Neogene. This suggests, once again, that the first three factors, and the “great evolutionary faunas” they represent, provide an adequate first-order description of the composition and size of marine faunas through the Phanerozoic.

The curve for total diversity in Fig. 5 suggests that the Phanerozoic can be divided into three basic intervals, each characterized by a different “style” of diversification. These intervals are (1) the Cambrian Period, encompassing the Ear-

ly Cambrian radiations and Mid to Late Cambrian diversity "plateau"; (2) the later Paleozoic interval, including the Ordovician radiations and the Silurian to Permian plateau; and (3) the post-Paleozoic or Mesozoic-Cenozoic interval, encompassing the general rise in diversity from the Early Triassic low to the Neogene high. These intervals are, of course, very similar to the three "multiple equilibria" observed by Bambach (1977) in his study of within-community species richness through the Phanerozoic (see also Newell 1967; Cutbill and Funnell 1967; Sepkoski 1979). This basic similarity in pattern from two very different data bases suggests that the triad of diversity intervals is a robust feature of Phanerozoic evolutionary history. Differences in pattern between Bambach's species-richness data and the taxonomic diversity data in Fig. 5 originate principally from two sources: (1) the higher stratigraphic resolution of the taxonomic diversity data (stage-level as opposed to system-level resolution), which shows that the Ordovician and Jurassic are transitional periods associated with the Paleozoic and post-Paleozoic intervals, respectively (this cannot be easily seen when all data from these systems are averaged); and (2) sampling biases specific to the taxonomic diversity data, especially the "pull of the Recent" (Raup 1978b, 1979a), which, as a result of the essentially perfect record from the modern oceans, causes taxa from the younger part of the Phanerozoic to have stratigraphic ranges that are extenuated (or, more accurately, less truncated) than taxa from older parts (see also Cutbill and Funnell 1967; Raup 1972). This sampling bias probably causes the rise in diversity toward the Recent to be over-accentuated in Fig. 5. A more accurate picture of the pattern (but not magnitude) of the post-Paleozoic diversification might be obtained if the diversity curve from the Jurassic and Early Cretaceous were simply extrapolated along the upwardly convex trend to the Recent, producing the third "multiple equilibrium" seen by Bambach (1977).

The scaling of the three factors to total diversity shows that each of the major evolutionary faunas is associated with, and perhaps even the cause of, a specific phase of diversification and "equilibrium." The Cambrian fauna (Factor I) clearly dominates the first phase. How-

ever, with the onset of the Ordovician radiations, the Cambrian fauna quickly declines and becomes unimportant by the late Paleozoic Era. The Ordovician radiations appear to be largely associated with the diversification of the Paleozoic fauna (Factor II), which is the primary contributor to the new, higher familial diversity that lasts until the end of the Paleozoic Era. But the modern fauna (Factor III) also becomes a significant constituent during the Ordovician radiations and, in fact, seems to grow very slowly in diversity throughout the remaining 200 Myr of the Paleozoic Era.

The importance of the Late Permian extinctions in shaping Phanerozoic history is very evident in Fig. 5. Not only is familial diversity reduced by nearly 50% during this event (cf. Raup 1979b) but a major turnover in taxonomic composition is also effected (cf. Raup 1976; Thayer 1979), with the modern fauna rapidly expanding to dominance. Thus, the Permian extinctions would appear to have been somewhat selective, affecting members of the previously dominant Paleozoic fauna to a greater degree than members of the slowly growing modern fauna. The modern fauna appears to be largely responsible for the growth of diversity subsequent to the Permian extinctions; the remnants of the Paleozoic fauna do contribute a minor amount to total diversity through the Mesozoic Era but appear to decline rapidly through the Cenozoic.

The pattern of growth and decline of faunas evident in Fig. 5 is broadly suggestive of displacement among the three great faunas of the Phanerozoic. In an analysis of early Phanerozoic marine families (Sepkoski 1979), I found that changes in diversity between the Cambrian and Ordovician Periods could be described quantitatively by a pair of coupled logistic curves. The mathematics indicated that if two faunas had different diversification rates and equilibria, the fauna with the higher rate and lower equilibrium could initially dominate the system; however, after a slow start, the fauna with the higher equilibrium diversity could grow very quickly, displacing the first fauna and causing it to decay exponentially to zero. This pattern appears to some extent in the interaction between the Cambrian and Paleozoic faunas in Fig. 5, particularly in the exponential

decay of the former shortly after the “equilibrium” diversity of the Cambrian is exceeded during the Ordovician radiations. What is not so evident is the slow but steady growth of the Paleozoic fauna throughout the Cambrian Period (see Sepkoski 1979, Fig. 7).

A slow if irregular increase in the modern fauna during the “equilibrium phase” of the Paleozoic fauna is evident in Fig. 5, suggesting a similar kind of displacement interaction might have existed between these two faunas. But what is more suggestive is the behavior of the Paleozoic fauna after the Permian extinctions. The fauna falters during the Triassic (although the irregularity of the curve may reflect simple statistical error) and falls to a minimum diversity during the Late Triassic extinctions. But then the Paleozoic fauna begins to rediversify during the general rebound from the extinction event and continues to diversify until the Late Jurassic-Early Cretaceous interval (near the beginning of Vermeij's [1977] “Mesozoic marine revolution”) when total familial diversity finally exceeds the level of the apparent Paleozoic equilibrium. Afterwards, the Paleozoic fauna appears to decay in a roughly exponential fashion, just as the Cambrian fauna did after its equilibrium was exceeded during the Ordovician Period.

These patterns are suggestive, but certainly not definitively indicative, of displacement of the Paleozoic fauna by the modern fauna in a manner not unlike the earlier displacement of the Cambrian fauna by the Paleozoic. The main differences between the two interactions are that the Paleozoic-modern interaction involved more kinds of animals, slower rates of replacement, and, of course, interference from the Permian and Triassic extinction events. The actual nature of these differences, and indeed the plausibility of the entire displacement hypothesis, must remain vague until further analysis can be made of the groups involved, their rates of diversification, and the biases affecting their appearance in the fossil record. However, it should be noted that this hypothesis is consistent with ideas by Thayer (1979) and Vermeij (1977) on ecological causes for the decline of the Paleozoic fauna (see also Meyer and Macurda 1977; Stanley 1977, 1979). These authors have suggested that increasing intensity of disturbance by bioturbation (“bulldozing”) and of predation by a slowly diversifying modern fauna may have led to the demise of the epifaunal suspension feeders that dominated the Paleozoic fauna. The patterns of diversification evident in Fig. 5 thus could be considered a map of this ecological displacement.

Patterns at Other Taxonomic Levels

The simplicity of pattern produced by the factor analysis of families within classes seems to suggest, at first encounter, an underlying simplicity to the Phanerozoic history of life in the seas. However, it might be possible that this simplicity is spurious, reflecting the taxonomic categories selected for analysis rather than any actual evolutionary patterns. More specifically, it might be that the small number of factors needed to explain the clade data is mostly a function of the long durations and mild temporal fluctuations in the sizes of the large classes that dominate the data.

To test this possibility, I repeated the entire analysis on numbers of marine families within metazoan *orders*. This increased the number of variables from 90 to 384 and decreased the average duration of the taxa from approximately 300 Myr to just under 200 Myr. Both of these changes served to increase the total amount of variance in the data set considerably. However, the results of factor analyzing the families within orders were very similar to those reported above. The first three factors, which again formed a distinct group on the scree graph, were almost identical in stratigraphic distribution to those illustrated in Fig. 3, although now accounting for about 11% fewer data (i.e. 79.3% vs. 90.8%). Again, loadings were positive or near zero over all 63 stratigraphic intervals and more than 90% of the large (i.e. greater than $|\pm 0.05|$) scores for the orders were positive. Thus, these three factors represent the same three great evolutionary faunas that seem to pervade the diversity data.

However, as opposed to the analysis of families within classes, the three “big” factors for families within orders began to break up as more and more factors were added and rotated. For example, an eight-factor solution, which accounted for almost 95% of the ordinal-level data, contained “remnants” of the three great

faunas (together accounting for 65.7% of the data) as well as a Tommotian factor (3.0% of the data; cf. Factor IV above) and four more factors apparently relating to major evolutionary radiations; these were a Lower Cambrian factor (4.4%), an Ordovician factor (4.6%), a Triassic factor (3.5%), and a Cenozoic factor (13.5%). The last three of these factors were very similar in stratigraphic distribution to the positive portions of Factors V and VII in Fig. 4. However, in the analysis of families within orders, the new factors were allotted greater statistical importance and received positive large scores from many more taxa so that they appeared like evolutionary faunas of secondary importance rather than simple variations upon themes. This was not true of factors beyond eight, which had smaller, nondominant loadings with both positive and negative signs; these minor factors picked up the small temporal contrasts within both the primary and secondary evolutionary faunas.

Summary

The nature of faunal change that is represented in taxonomic data drawn for the Phanerozoic marine fossil record seems to be rather simple. Factor analysis suggests that much of the temporal variation in the number of families within metazoan classes, and within metazoan orders, can be accounted for by assembling the marine taxa into three great evolutionary faunas:

- I. A Cambrian fauna that dominates the Cambrian fossil record but decays rapidly in importance during the post-Cambrian portion of the Paleozoic Era;
- II. A Paleozoic fauna that is present during the Cambrian Period but grows in importance primarily during the Ordovician and remains dominant until the Permian extinctions at the close of the Paleozoic Era;
- III. A Mesozoic-Cenozoic, or "modern," fauna that first attains appreciable diversity during the Ordovician radiations, grows slowly in importance throughout the remainder of the Paleozoic Era, and then ascends rapidly to dominance with the Permian extinctions; this is still the dominant evolutionary fauna in the oceans today.

There is some turnover in taxonomic composition within each of the three evolutionary faunas during their periods of dominance, but this seems to be only "background" change that is minor compared to the magnitude of change during the ascent and decline of the major faunas.

Each evolutionary fauna appears to be associated with a distinct phase of diversification in the world ocean. The Cambrian fauna is associated with (or, is responsible for) the radiations of the Early Cambrian Period and the diversity plateau of the Mid to Late Cambrian; the Paleozoic fauna is associated with the Ordovician radiations and the long Paleozoic equilibrium; finally, the modern fauna is associated with the rebound from the Permian and Triassic extinctions and the subsequent maximum in marine diversity. During periods of expansion of new faunas, the previously dominant fauna decays away in a manner suggestive of displacement. Thus, the Cambrian fauna declines approximately exponentially as the expanding Paleozoic fauna increases diversity beyond the level of the Late Cambrian Period; the Paleozoic fauna then behaves similarly during the Mesozoic-Cenozoic interval but only after expansion of the modern fauna increases diversity above the approximate level of the Paleozoic equilibrium. These patterns of diversity may reflect ecological displacement of each evolutionary fauna by its successor.

Acknowledgements

I thank Christopher Scotese for his generous assistance in producing Fig. 1 on the CALCOMP Plotter.

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