PATTERNS OF TAXONOMIC AND ECOLOGICAL STRUCTURE OF THE SHELF BENTHOS DURING PHANEROZOIC TIME

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ABSTRACT. The taxonomic and ecological structure of the shelf biota are intimately related at the species–population levels. Early Paleozoic faunas contained relatively few species representing relatively many higher taxa, and ecosystems were relatively generalized. Medial and late Paleozoic faunas contained more species representing fewer higher taxa, and ecosystems were relatively specialized. This suggests that, as higher taxa became extinct, they were not replaced except at lower taxonomic levels; diversification was proceeding through increasing specialization. After Permo-Triassic extinctions, rediversification was chiefly confined to low taxonomic levels. Late Mesozoic and Cenozoic diversification at lower taxonomic levels has been remarkably great, resulting not only from increasing specialization at the population level but from a marked increase in provinciality due to rising latitudinal temperature gradients on the shelves and to the fragmentation and isolation of shelf environments by continental drift.

THIS paper examines the historical relationships between the ecological and taxonomic structures of the marine biosphere, and attempts to account in a general way for the patterns of their evolution. Each of these structures is hierarchic. The units composing the levels of the ecological hierarchy include individuals, populations, communities, and provinces, while the units composing the levels of the taxonomic hierarchy are such categories as species, genera, and families.

There has been relatively little theoretical discussion of the evolution of these structures for marine invertebrates, yet the geological record of skeletonized taxa of the shallow marine invertebrate benthos is longer and more complete than for any comparable group of organisms. This paper therefore deals with the rich and lengthy record of shallow marine environments.

This restriction to a specific group of communities has some special advantages. The diversity pattern for the world at large is obviously very much influenced by the deployment of organisms into new environments, such as the invasion of the terrestrial habitat by vertebrates. By restricting the data to a limited group of communities it may be possible to investigate the patterns of diversity changes within ecosystems.

Much of the structural evolution which the taxonomic and ecological hierarchies have undergone is a product of the diversification and extinction of species. There has been much discussion of the patterns of taxonomic diversifications and extinctions through geologic time, especially of higher taxa, and ecological relations are commonly invoked to account for these patterns, particularly for extinctions. The processes of diversification assumed herein are those of the synthetic theory of evolution based on Darwinian selection and upon modern genetic concepts. Speciation and the origin of higher taxa have been discussed from this viewpoint in a number of larger works (for example Huxley 1942; Mayr 1963; Rensch 1947; and Simpson 1953). As diversity rises, there must be a mechanism of accommodation of the new forms in ecological systems; such mechanisms are discussed by Klopfer (1962), MacArthur and Wilson (1967), and

Miller (1967), among others. Possible causes of extinction, and hypotheses of the processes of extinction that have operated to create the Permo-Triassic faunal change, have been reviewed by Rhodes (1967).

THE ECOLOGICAL STRUCTURE OF THE BIOSPHERE

The ecological hierarchy is regarded as being composed of the levels that are depicted in text-fig. 1. This paper is chiefly concerned with the functional aspects of the hierarchy,

| GENETIC HIERARCHY		ECOLOGICAL HIERARCHY		
UNIT	COLLECTIVE	DESCRIPTIVE UNITS	FUNCTIONAL UNITS	LEVEL
$*^2$	$*^3$	Marine Shelf Biota	Shelf Realm of the Biosphere	High
$*^1$	$*^2$	Province	Provincial System	
Gene Pool	$*^1$	Community	Community System (Ecosystem)	
Genotype	Gene Pool	Population (Deme, Species)	Population System (Niche)	
Functional Genetic Unit	Genotype	Individual	Ontogenetic System	Low

$*^1$ Collection of gene pools
$*^2$ Collection of gene pool collections
$*^3$ Collection of collected gene pool collections

TEXT-FIG. 1. Some levels of organization in the ecological hierarchy employed in this paper (after Valentine 1968b).

that is, with the interacting systems of organisms and environments. From the highest level down, each functional system is composed of subsystems representing the systems of the next lower level. The lowest functional level in the figure, that of the individual, is certainly capable of further subdivision into sorts of functions of 'unit characters', each underpinned by a system of genes and its regulators. For the most part, however, the present discussion concerns population and higher levels.

It is convenient to consider the ecological units in terms of the environment with which they interact. Hutchinson (1957, 1967) has developed a formal conceptual model that treats the environment as a multi-dimensional region (see also Simpson 1944, 1953). Only an informal treatment, based on Hutchinson's model, is required here. If each separate environmental parameter is visualized as a single geometric dimension of this region, then all possible environments are represented by the resulting multi-dimensional

space or hyperspace, which contains as many dimensions as there are possible environmental parameters. The space extends along each dimension to the physical limits of each parameter. It is assumed that this multi-dimensional environment model is standardized by having each axis allotted an arbitrary but permanent direction to form an
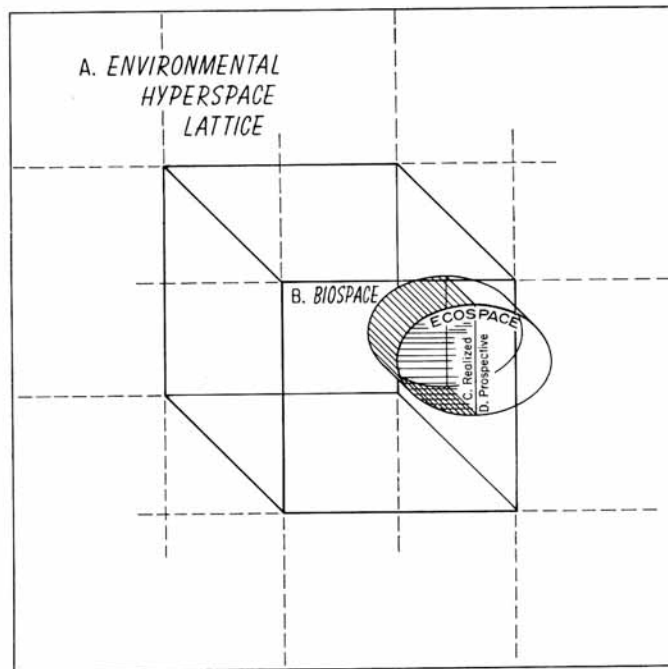
TEXT-FIG. 2. Highly diagrammatic representation of some aspects of environment–organism relations, visualized as a multi-dimensional space, of which each dimension is some environmental factor, physical or biotic. Each point within the lattice represents a unique combination of factors. Only three of the many dimensions are depicted. A, the total possible range of all environmental factors represented as a multi-dimensional lattice. B, the portion of the environment that actually exists on earth, the *biospace*; it is available for occupation by organisms. C and D, the region of environmental space that coincides with factors tolerated by an organism and that is bounded by its limits of tolerance— the *ecospace* of the organism. Only a portion of the ecospace is realized (C); the remainder is prospective ecospace (D) that may be inhabited if the environment fluctuates so as to include more of that portion of the lattice. The ecospace concept may be expanded to population, community, province or biosphere levels, and to species, genus, family, and higher taxonomic levels.

environmental hyperspace lattice, hereinafter called simply a lattice for brevity. Only a certain portion of the total possible lattice (the prospective lattice) actually represents conditions of the environment. This 'realized ecological hyperspace' may be called *biospace* (text-fig. 2), a term employed in a similar but less generalized sense by Doty (1957).

For any organism there is some more or less small volume (actually a hypervolume)

within the lattice corresponding to the range of environmental conditions under which it may live. This functional hypervolume will be called the *ecospace* of that organism (text-fig. 2). Each population also has its own ecospace, which is the hypervolume of its niche within the lattice. Indeed, the ecological units at all levels have ecospaces. A community ecospace is the multi-dimensional model of its ecosystem, and a provincial ecospace is the model of the provincial system. Although the highest functional level standing above that of the provincial system is the level of the biosphere, the system of the shallow marine realm is being used here in its place as a matter of simplicity, and this realm has its own ecospace. The total ecospace that an organism or other ecological unit may utilize if it is physically available may be called the *prospective ecospace*, while the portion of the ecospace that actually overlaps with realized biospace may be called the *realized ecospace*. These terms are modelled on the discussion of Parr (1926) and Simpson (1944, 1953).

Dimensions of the lattice which have special properties are those that represent the *real* dimensions of space, in which discontinuities occur that permit the occupation of similar functional regions in different geographic regions (Miller 1967) and of time, in which the changing shapes and sizes of ecospaces and of biospace are perceived.

The structure of the ecological hierarchy may be illustrated by considering just one level, for example the community level. Community ecospace is composed of the ecospaces of all the niches of the component populations, and includes some dimensions that are not niche properties but are organizational properties of the ecosystem. The size of the community ecospace, measured by the number of dimensions occupied and the extent of occupation along each dimension, depends upon the sizes of the component niche ecospaces and to a small extent upon the organizational properties. Into a community ecospace of a given size, a relatively large number of small niches or a relatively small number of large niches may be packed. All niches in a community ecospace overlap to some degree, for all share a common tolerance for certain salinity ranges, for example, and for certain oxygen concentrations, and for other parameters. The more that niches overlap, other things being equal, the more populations that can be packed into a community ecospace of a given size (Klopfer 1962; Miller 1967).

Consider, then, a community (*A*) composed of relatively few populations that have very large niches that overlap only narrowly on the whole. The animals tend to be rather generalized feeders, so that energy flows in relatively broad streams through the trophic levels. This community, though of low diversity, may displace a large biospace in the lattice, that is, may have a large ecospace. Consider another community (*B*) composed of many populations of different species that tend to have very small niches which overlap broadly on the average. The animals are highly specialized with relatively narrow ranges of food sources, so that energy flows through the trophic levels in relatively discrete paths along chains of organisms that tend to be rather isolated owing to their high specialization. Energy flow is not like a stream but more like a shower that breaks up into numerous jets. A community of this sort, though rich in species, may displace no more biospace in the lattice than community (*A*) and may displace considerably less.

These communities have vastly different structures in the lattice, and yet it seems possible for one to evolve from the other. They may thus represent relatively early (*A*) and advanced (*B*) stages in the evolution of a community 'lineage' that has inhabited

a similar biotope through its history. In this event the ecospaces of the two communities will approximately coincide, although the way in which each community biospace is occupied by niches is different. The community structure has evolved.

Structural states of ecological systems at other levels may be described in an analogous way. All the systems evolve by changes in the quality, relative proportions, and diversity of their subsystems (Valentine 1968b). Thus evolution of ecological systems need not involve organic evolution, but may result merely from the readjustment of existing populations in new patterns of association. However in the present discussion the chief interest lies in changes that *are* based upon organic evolution, upon changes in gene frequencies within populations that produce changes in niches, and upon the accommodation of the changed niches in ecosystem structures. Enough is now known of these processes to permit the construction of a provisional model of the diversification of ecosystems. But before proceeding to the model, it is appropriate to examine the main patterns of taxonomic structure during the Phanerozoic.

## THE TAXONOMIC STRUCTURE OF THE BIOSPHERE

The taxonomic hierarchy is too well known to require any general remarks. For purposes of this paper only a few levels need be considered: phylum, class, and order, which will be called 'higher' taxonomic categories; and family, genus, and species, which will be called 'lower' categories. It is possible to visualize the ecospace of any genus as composed of the ecospaces displaced by all its component species, and the ecospace of a family as composed of all the generic ecospaces, and so on. Thus defined, the ecospace of a higher taxon displaces the actual regions of the lattice that have been occupied by the members of that taxon. Thus the taxonomic hierarchy possesses a precise structure at any time. This structure changes through time in well-defined patterns.

The main trends of evolution of the taxonomic structure may be characterized by considering the trends of diversity among higher and lower taxa through geologic time. The fossil record of diversity, however, is certainly biased. An important source of bias is the differential preservation of taxa. It seems possible to use the skeletonized taxa that are best represented as a sample, from which to attempt to generalize to the entire biota. The basic data from which generalizations will be attempted are the records of easily fossilized shallow benthonic taxa of nine phyla: Protozoa, Porifera, Archaeocyatha, Coelenterata, Ectoprocta, Brachiopoda, Mollusca, Arthropoda, and Echinodermata. The ranges of these phyla and of their taxa are taken chiefly from the *Treatise on Invertebrate Paleontology* (ed. Moore 1953–67), the *Fossil Record* (ed. Harland *et al.* 1967), and the Russian *Osnovy Paleontologii* (Orlov 1958–64).

As the assignment of groups of organisms to taxonomic categories involves a large element of subjectivity, it is fair to ask to what extent the trends in taxonomic diversity are real. In the first place, if one constructs a hierarchical classification of fossils that appear at different times, the average time of appearance of higher taxa will be earlier than that of lower, simply because some of the lower taxa appeared later than others, but none appeared earlier than the higher taxa to which they belong. The mode of first appearance should shift progressively towards the present at lower and lower taxonomic levels (Simpson 1953, pp. 237–9). Similarly, the mode of highest diversity will tend to shift towards the recent at progressively lower levels provided that the earlier taxa at each

level persist or are replaced. These considerations account for such shifts in the mode of appearance and diversity in text-fig. 3.

Secondly, there is no doubt that the present data contain monographic artifacts (for
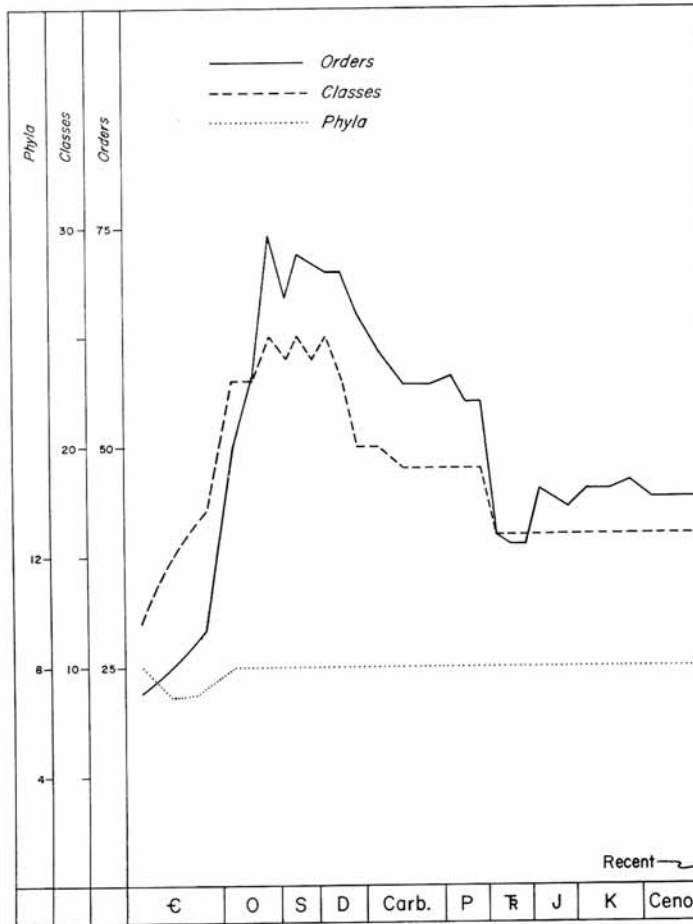
TEXT-FIG. 3. Stratigraphic variation in diversity of higher taxa of well-skeletonized marine shelf invertebrates. Data chiefly from Harland *et al.* (1967) and Moore (1953–7).

an instructive example see Williams 1957). However some of the main points to be discussed here concern relative diversities among the several taxonomic levels. Presumably, monographic artifacts would tend to appear at all levels, and relative diversities would be much less affected than absolute diversities. It is unlikely that there is a consistent

monographic bias in the same direction among a majority of the taxa, and I therefore believe that the major trends are real.

Another important consideration is the extent to which trends among skeletonized taxa represent the biota as a whole. At present the non-skeletonized Invertebrata have the same biogeographic and synecological patterns as skeletonized groups (Lipps, *in press*), and there is no reason to expect that patterns of diversity of non-skeletonized taxa would follow different trends than the skeletonized ones. Furthermore Lipps has pointed out (pers. comm.) that the preserved groups are morphologically diverse and unrelated, yet they often exhibit similar patterns. Therefore it is assumed that major trends among skeletonized and non-skeletonized groups tend to be in phase.

Experience has shown clearly that the chances of preservation of an organism that does not possess a well-mineralized skeleton are exceedingly small. Indeed, the lack of a record of a taxon that does not have a relatively high probability of preservation can hardly be taken as proof that the taxon was not living at the time. And the probabilities of preservation cannot yet be specified even for taxa with highly mineralized skeletons, under many of the stratigraphic situations common in the geologic record. It is therefore difficult to assess the significance of negative records.

Most of the known phyla had appeared in the record by Cambrian time, although even among our sample of nine, one (Ectoprocta) does not appear until the Lower Ordovician. The phyla are well-differentiated and some contain relatively complex organisms when they first appear, so that a fairly long period of evolution can be assumed to have preceded their appearance in the record. However, it is possible to argue for many phyla that their final organization into the ground-plans that are now considered as characteristic may have only narrowly preceded their appearance in the record (Cloud 1949, 1968). It has been suggested that such a great evolutionary event may have been permitted by an increase in atmospheric oxygen past a critical level (Berkner and Marshall 1965). At any rate, it is likely that nearly all of the invertebrate phyla had become established before the Cambrian, and the relative timing of their appearance in the record may partly indicate the order in which they acquired hard parts or the chance occurrences of unusual preservations. Nicol (1966) and others have suggested that the acquisition of hard parts may have ensued as a result of widespread phyletic body-size increases.

Many of the nine phyla in the sample contain taxa that are not members of the shelf benthos or that have relatively low probabilities of preservation. Examples are the planktonic Scyphozoa and the soft-bodied Keratosa. Such taxa are excluded from the tallies. A few other taxa probably participated only partly in the benthonic ecosystems. An important example is the Ammonoidea. The effects of such taxa on the diversity curves are considered separately. Diversity graphs for phyla, classes and orders that seem to be chiefly members of the benthos are presented in text-fig. 3; diversities are classed by geological epochs, and therefore do not exactly represent the standing diversities at any given time. The diversity levels depicted in text-fig. 3 represent a balance between diversification and extinction, but the amount of taxonomic turnover that has occurred in any epoch cannot be inferred from the diversity levels. Text-fig. 4 depicts the numbers of appearances and disappearances (presumed to be extinctions) among the higher taxa per epoch.

From text-figs. 3 and 4 the following history of higher taxonomic diversity can be

inferred. The higher the category the earlier it tends to reach its maximum diversity. If the phyla were not all present throughout the Cambrian, at least they all appear by early Ordovician time, but the highest diversity is recorded in the Middle and Upper Cambrian. New classes continue to appear until the Lower Carboniferous, but the highest class diversity is recorded in the Middle and Upper Ordovician. Orders have
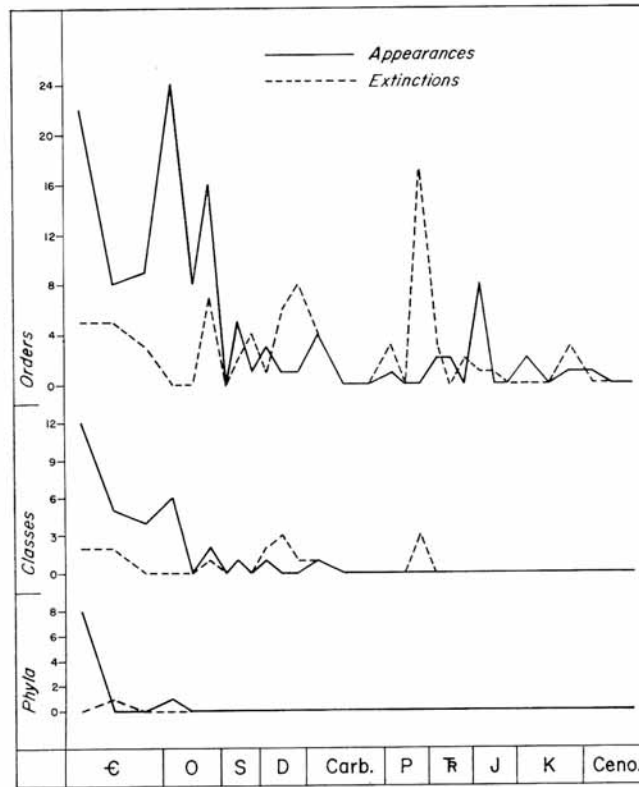

TEXT-FIG. 4. Appearances and extinctions of phyla, classes and orders of shelf benthos in the sample, classed by Epochs. Data as in text-fig. 3.

continued to appear until the end of the Cretaceous, but achieved their highest recorded diversity in medial Ordovician time. Ordinal diversification, however, was great during early Ordovician time, whereas the greatest class diversification was during the Cambrian (text-fig. 4).

It also appears that the higher the taxonomic category the less it has been ravaged by extinction, and the earlier extinction has stopped. Only one phylum (Archaeocyatha), which comprises 11% of the sample, disappears, although the sample is so small that this figure cannot be taken as very precise. However, 16 classes comprising 50%, and

75 orders comprising 64%, disappear. These extinct taxa are never fully replaced by other higher taxa, at least not from among the taxa that we are considering, so that the diversity of each higher taxonomic category has decreased, rather markedly in the cases of classes and orders, since the early Paleozoic. For the taxa in the sample, the extinction of phyla is complete by the end of Cambrian time, of classes by the end of Permian time, and of orders by the end of the Cretaceous.
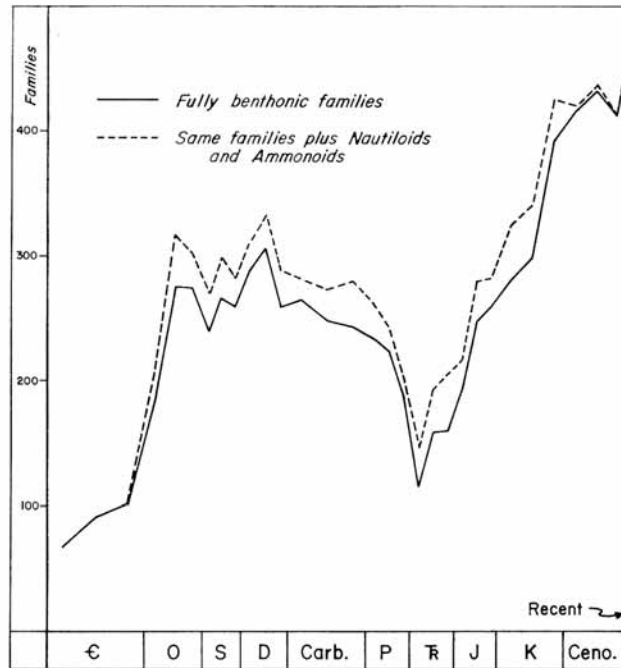
TEXT-FIG. 5. Stratigraphic variation in diversity of skeletonized families of shelf benthos belonging to phyla included in text-fig. 3. Data chiefly from Harland *et al.* (1967), Moore (1953–7), and Orlov (1958–64)

The lower taxa present a somewhat different pattern. Text-fig. 5 depicts the geological record of family diversity in the sample, again excluding unsuitable taxa such as the planktonic foraminiferal families, and text-fig. 6 depicts the record of appearances and disappearances. About 100 families are recorded by the end of the Cambrian, and 300 occur in the Upper Ordovician; diversity remains near 300 until the later Paleozoic, when it gradually falls off. A marked drop occurs in late Permian and early Triassic times. The pattern has until this point been not too unlike that of the higher taxa, with the mode of major diversity shifted towards the present. The Jurassic rise is even anticipated on the ordinal level (text-fig. 3). However it is in the great diversity rise of the Cretaceous and Cenozoic that the pattern of the families departs in a fundamental way
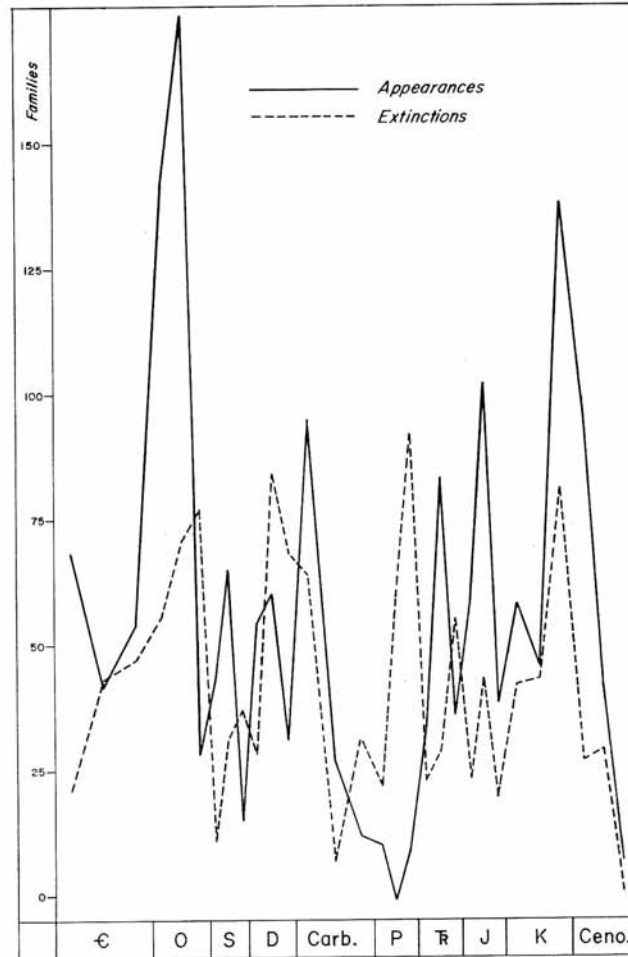
TEXT-FIG. 6. Appearances and extinctions of the families of shelf benthos in the sample, including Nautiloidea and Ammonoidea, classed by Epochs. Data as in text-fig. 5.

from the pattern of the higher taxa, for the higher taxa reach and maintain rather steady levels of diversity from Ordovician onwards for phyla, Lower Triassic onwards for classes, and lower Jurassic onwards for orders. The Cretaceous and Cenozoic diversification of families marks a major change in the evolutionary trends of taxonomic structure.

It can be seen from text-fig. 6 that the times of diversification of families tend to alternate with times of extinction. This pattern is well shown in a figure by Newell (1967,

fig. 7) that is based upon a different taxonomic sample. The pattern certainly suggests that times favourable for diversification and those favourable for extinction were distinct, and that there is therefore a complementary relation between these processes. Newell suggests in effect that there have been extinctions to provide unoccupied biospace before there are major diversifications, and of course there must be many taxa resulting from diversification before there can be major extinctions. However, the data in text-figs. 5 and 6 do not entirely bear out this thesis. The very high extinction peaks in the Ordovician, Devonian, and Cretaceous are not accompanied by massive reductions in standing diversity. In fact, the early Ordovician and Cretaceous extinction highs are nearly hidden in text-fig. 5 owing to the great contemporary diversifications. Late Ordovician and Devonian extinction peaks reduce the diversity level somewhat, but only by about 6 and 13% respectively, because diversification is fairly high at these times. Only near the Permo-Triassic boundary, when diversification is exceedingly low (text-fig. 5), does the diversity level suffer a major decline of about 50%. The unusually low level of Permo-Triassic diversity is not unique because of the extinction peak alone, but because of the lack of a corresponding peak of diversification.

It is interesting to examine the patterns of family diversification and extinction within each of the higher taxa. Newell (1967) has presented graphs of family diversification among a number of higher taxa; I have prepared similar charts for diversification as well as for extinction of the families of higher taxa in the present sample which confirm the patterns he has presented. In general, however, the high rates of family diversification and of extinction within a higher taxon do not alternate in time but are highly correlated. For example, the Brachiopoda diversify strongly during the Ordovician and Devonian, but extinction peaks are found at these times also. Secondary levels of diversification during the Silurian and Lower Carboniferous correlate with secondary peaks of extinction. Only in the Permian is there a lack of correlation; the great extinction is not accompanied (nor is it followed) by diversification at the family level, but is accompanied by the lowest diversification rate known for brachiopods during the Phanerozoic.

Trilobites display a similar correlation. Cambrian diversification rises to a peak in the late Cambrian and falls off progressively during Ordovician epochs; extinction levels do precisely the same, except that they rise a bit in latest Ordovician. There is no following rise in diversity, however, although there is a secondary peak of extinction in medial and late Devonian time. Certainly there is no alternation of diversification and extinction. The same may be said of diversity patterns of the Porifera, the Echinoidea, and several of the Paleozoic echinoderm groups. The Foraminiferida, Anthozoa, and Gastropoda have more complex patterns, but there is no suggestion of alternating extinction and diversification except at the Permo-Triassic boundary. In the Ostracoda there is some indication that extinction follows diversification and not the reverse, and similar trends are found during parts of the record of other taxa. Even in the Ammonoidea and Nautiloidea peaks of diversification and extinction tend to correlate and certainly do not alternate.

The alternation of peaks of diversification and extinction of all families in the sample (text-fig. 6), then, are chiefly due to the alternation of high rates of family extinction of some higher taxa with high rates of diversification of different higher taxa (which is usually accompanied by a rise in extinction among these different taxa also). Except at the Permo-Triassic boundary, all this tends to be accomplished while diversity as a whole

remains surprisingly stable considering the magnitude of extinction and diversification peaks. The major events that alter standing diversity on the family level are the diversification in Cambro-Ordovician times, the Permo-Triassic diversity low, and the Cretaceous–Cenozoic diversification (text-fig. 5).
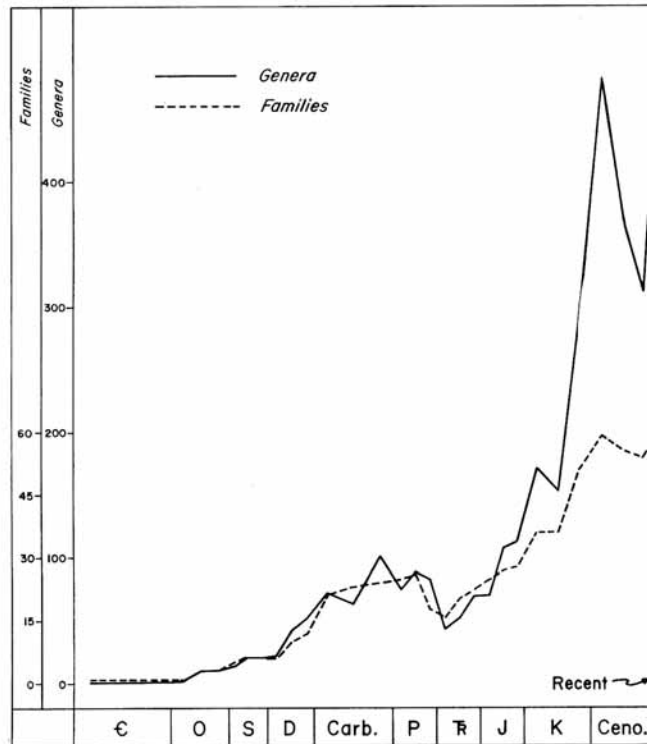
TEXT-FIG. 7. Stratigraphic variation in the diversity of benthonic shelf families (dashed line) and genera (solid line) of Foraminiferida, excepting the poorly skeletonized Allogromiina. Data from Loeblich and Tappan (1964).

It is possible to demonstrate that with the genera as with the families, there is a striking rise in numbers in the Cretaceous and Cenozoic. Text-fig. 7 depicts the diversity of families and of genera of benthonic Foraminiferida through geological time. This is one of the taxa that contributes strongly to the late Cretaceous and Cenozoic rise in family diversity. Throughout the Paleozoic there are, on the average, about 3–4 genera per family described. Across the Permo-Triassic boundary this ratio drops and then rises again in the Jurassic and early Cretaceous. In the late Cretaceous the genus/family ratio climbs to nearly 6, and in the early Cenozoic to over 8, where it stands at present after a late Cenozoic decline. The size of families is somewhat a matter of opinion. There is no

special reason, however, to believe that the disproportionate Cretaceous–Cenozoic rise is a taxonomic artifact. The data are certainly subject to monographic and other biases, but have all been reviewed by the same team of authorities (Loeblich and Tappan 1964). It is interesting in this regard that the same trend can be inferred from the data charted by Henbest (1952) based chiefly on the work of Cushman (1948). If the trend is an artifact it is an enduring one. Incidentally, peaks of extinction of genera of foraminiferida correlate rather than alternate with peaks of diversification, just as is common among invertebrate families.

Another taxon that contributes heavily to the Cretaceous rise in family diversity is the Gastropoda, among which the same pattern of disproportionate generic diversification is present. There is no satisfactory recent review of all marine gastropod genera,

| ORDERS	GEOLOGIC RANGE	FAMILIES	Genera & Subgenera	Genera – Subgenera / Family
Archaeogastropoda[1]	U. Cambrian–Recent [2]	82	1314	16.0
Mesogastropoda	U.Ord. (Caradocian)–Recent	75	1467	19.6
Opisthobranchia	L.Carb. (Visean)–Recent	9	240	26.6
Neogastropoda	L. Cretaceous (Albian)–Recent	20	1119	56.0

[1] Including Bellerophontacea.

[2] Possibly from L. Cambrian, depending upon ordinal assignment of early groups.

TEXT-FIG. 8. Families, genera, and subgenera of orders of shallow marine gastropods. The most advanced orders contain higher numbers of genera and subgenera, on the average, than primitive orders. Data from Taylor and Sohl (1962).

but Taylor and Sohl (1962) have published a census of gastropod genera and subgenera combined by family and higher taxa. It is possible to show that the more recently an order has appeared in the record, the more genera and subgenera per family it contains on the average (text-fig. 8). The Neogastropoda, which appear in the Lower Cretaceous (Albian or possibly earlier) and which diversify chiefly in the Upper Cretaceous and later, have 56 genera and subgenera per family on the average. This is $3\frac{1}{2}$ times as many as the average of the Archaeogastropoda. Furthermore, even the groups of archaeogastropods with the largest living representatives, such as the trochaceans, tend to have differentiated strongly at the generic level in the Upper Cretaceous and Cenozoic. For the Trochacea, for example, there are 14 genera and subgenera recorded from the Lower Cretaceous, 32 from the Upper Cretaceous, and 66 from the Upper Cenozoic (data from Moore 1953–7). The other orders of Gastropoda are intermediate, both in time of appearance and in genus–subgenus/family ratios, between the Archaeogastropoda and the Neogastropoda. It follows from this situation that, for the shallow marine shelled Gastropoda, the late Cretaceous–Cenozoic rise in family diversity (from 37 families in the Lower Cretaceous to 66 in the Upper Cretaceous and to 83 or 84 in the Cenozoic) is disproportionately exaggerated on the generic level. This agrees with the data for Foraminiferida. Two other groups that contribute especially strongly to the rise in Upper Cretaceous and Cenozoic family diversity, the Ectoprocta and the

Echinoidea, appear to display similar trends (see Newell 1952 and the appropriate *Treatise* volumes).

In contrast to the preceding groups, the phylum Brachiopoda displayed its greatest familial diversity during the Paleozoic. It has not diversified during the Cretaceous–Cenozoic but maintained an average of about 12 or 13 families and about 50–65 genera
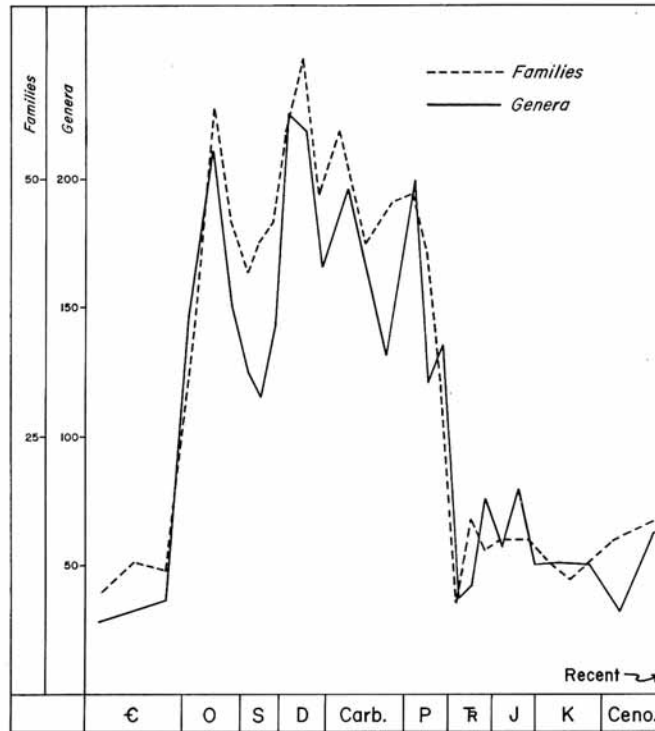
TEXT-FIG. 9. Stratigraphic variation in brachiopod diversity by families (broken line) and by genera (solid line). The genera/families ratio remains near 4. Genera after Williams (1965), and family data from Williams *et al.* (1965).

during this time (text-fig. 9). It is interesting, therefore, that the brachiopods have about the same genus/family ratio recorded for the Paleozoic as in the Mesozoic and Cenozoic —about 4 times as many genera as families throughout the Phanerozoic. Even during the greatest periods of diversification, the numbers of genera per family did not rise disproportionately, although generic turnover was significantly greater than family turnover. Judging from a comparison of the graphs of evolutionary rates among trilobite genera (Newell 1952) with family diversity trends, disproportionate generic diversity is not found among trilobites during their time of greatest family diversity either.

In summary, diversification on the family level during the Paleozoic and early Mesozoic

seems to be accompanied chiefly by simple proportionate diversification on the generic level. Diversification on the family level during the late Cretaceous and Cenozoic seems to be accompanied by a disproportionately high diversification on the generic level.

It is impracticable to attempt a census on the species level for even a few higher taxa, and there are strong reasons for doubting the significance of fossil species counts in any event. It is necessary to approach species diversity at least in part from a theoretical point of view. Species evolve at greater frequencies than genera or families or higher taxa, and their standing diversities are therefore more volatile. The appearance of isolated habitats can produce swarms of closely related species, and the development of specialized communities may permit the development of a great number of species, not necessarily closely related, but endemic to the community. Reef communities, for example, appear to contribute large opportunities for both these types of speciation. A great number of specializations are possible on reefs, and thus large numbers of relatively specialized species from various phylogenetic backgrounds may appear. Reef tracts are also characterized by patchy and discontinuous distributions of reefs, and the isolation of outlying patches might often serve as a basis for speciation. Communities such as those on reefs that appear, endure long enough for a highly specialized biota to develop, and then disappear or become greatly reduced, can produce temporally localized but significantly large fluctuations in standing species diversity. If species diversification is great within such communities, generic diversity would also be enhanced. Since the species endemic to such communities are normally specialized, the average niche size of the shelf biota would be decreased while they flourish and increased when they wane.

At times the middle and upper Paleozoic record contains numerous reef associations and at these times it is likely that species diversity reaches disproportionately high levels, relative to families. It is expected that generic diversity might also rise disproportionately at these times. Although early and middle Permian reefs are widespread and contain probably the most specialized Brachiopoda recorded (Rudwick and Cowen 1968), a disproportionate generic diversity peak does not appear at that time in the available data (text-fig. 9). The description and evaluation of Permian reef biota is far from finished, however.

Another important way in which specific (and generic) diversity may be disproportionately multiplied is through a rise in provinciality. For example, theoretical considerations suggest that there are many more shelf species today than in the past, owing to the high degree of shallow-water provinciality at present (Valentine 1967, 1968a). This provinciality is both latitudinal, correlating with the great latitudinal temperature gradients at present, and longitudinal, owing to the presence of efficient biogeographic barriers of continents and ocean deeps. In the early Jurassic provinciality was not strongly developed. A Middle and Upper Jurassic Boreal fauna that contains endemic forms has been widely recognized (Neumayr 1883; Arkell 1956). Evidence has now been advanced to suggest that the Boreal fauna of the Jurassic signifies a low-salinity facies in a region of rather stable palaeogeography rather than a climatic province (Hallam 1969). Whatever its environmental basis, the appearance of the widespread fauna marks an increase in environmental heterogeneity on a sub-continental scale and a rise in species diversity. The general trend towards increasing provinciality in late Cretaceous and Cenozoic times must have greatly enhanced the numbers of species on the shelves (Valentine 1967, 1968a). Many genera which contain several species in a given province

are now represented in different provinces by separate suites of species, so that the total numbers of their species are immense. Such is the case with species of *Nucula*, *Macoma*, and *Mactra* among the Bivalvia and *Conus*, *Calliostoma*, and *Fissurella* among the Gastropoda, to choose a few of the many examples. This situation must have been much less marked during times of low provinciality. For these reasons alone it is contended that the number of species in the shelf environment has increased disproportionately relative to the genera, especially during the Cretaceous and Cenozoic. Thus a species diversity curve would have about the same pattern as a generic diversity curve, but the peaks would be exaggerated (and the curve would be offset slightly towards the present). There are still other reasons, discussed below, for believing this pattern to be correct.

The major diversity trends in time among the fossil taxa are assumed to reflect real diversity trends among the ancient shelf biota, and they can be described in terms of the structure of the taxonomic hierarchy (text-fig. 10). In the earliest Paleozoic each phylum was represented by only a few classes, each class by relatively few orders, and so on down the hierarchy. By the close of Ordovician time, however, the average phylum was well differentiated into classes, and the average class into orders. Some phyla became extinct, but were not replaced by other phyla. After the Middle Ordovician the diversity of classes and of orders declined but the diversity of families rose, so that the structure became relatively more diversified among the lower taxa (text-fig. 10). It is possible that the average generic and specific diversity of the Upper Carboniferous indicated in text-fig. 10 is too low, owing to a disproportionate diversification at these lower levels that culminated during the early Permian. At about the Permo-Triassic boundary, both the numbers of classes and of orders were reduced by just less than half relative to their Middle Ordovician peaks, as were the families. The Permo-Triassic diversity low was most marked at lower taxonomic levels (contrast the familial and ordinal diversity decreases).

After the Permian the only gains in diversity registered among higher taxa are on the ordinal level. The numerous lost classes are not replaced, and even the rise in ordinal diversity is relatively small. The great climb in diversity at the familial level returns the hierarchy to a pattern commensurate with the early Upper Paleozoic pattern by Middle Jurassic time. Thereafter the number of families per higher taxon increases, especially during the Upper Cretaceous, and the diversities of lower taxa follow suit (text-fig. 10).

The so-called nekto-benthonic cephalopod groups Nautiloidea and Ammonoidea have not been included in the basic sample because of uncertainty as to the degree to which they participated in benthonic ecosytems. Nevertheless, some of them were surely regular members of a benthonic food chain. In text-fig. 5, the families of these cephalopod taxa are added to the families of the sample. The pattern of diversity is not much altered thereby; there was a slight increase in the steepness of the diversity rise from the Triassic to the Lower Cretaceous and the appearance of a rough plateau during the late Cretaceous and Cenozoic. The effect on the ordinal level is to emphasize the Ordovician rise in diversity and the mid- and upper-Paleozoic decline. Therefore, the exclusion of these Cephalopoda from the sample has a conservative effect insofar as the major trends are concerned, and in no way contributes to special conclusions.

Another major group which might have merited some representation in the figures is the fishes. At the family level their inclusion would raise the curve in text-fig. 5 to an even higher Devonian peak, and somewhat steepen the Mesozoic trend of rediversification (as
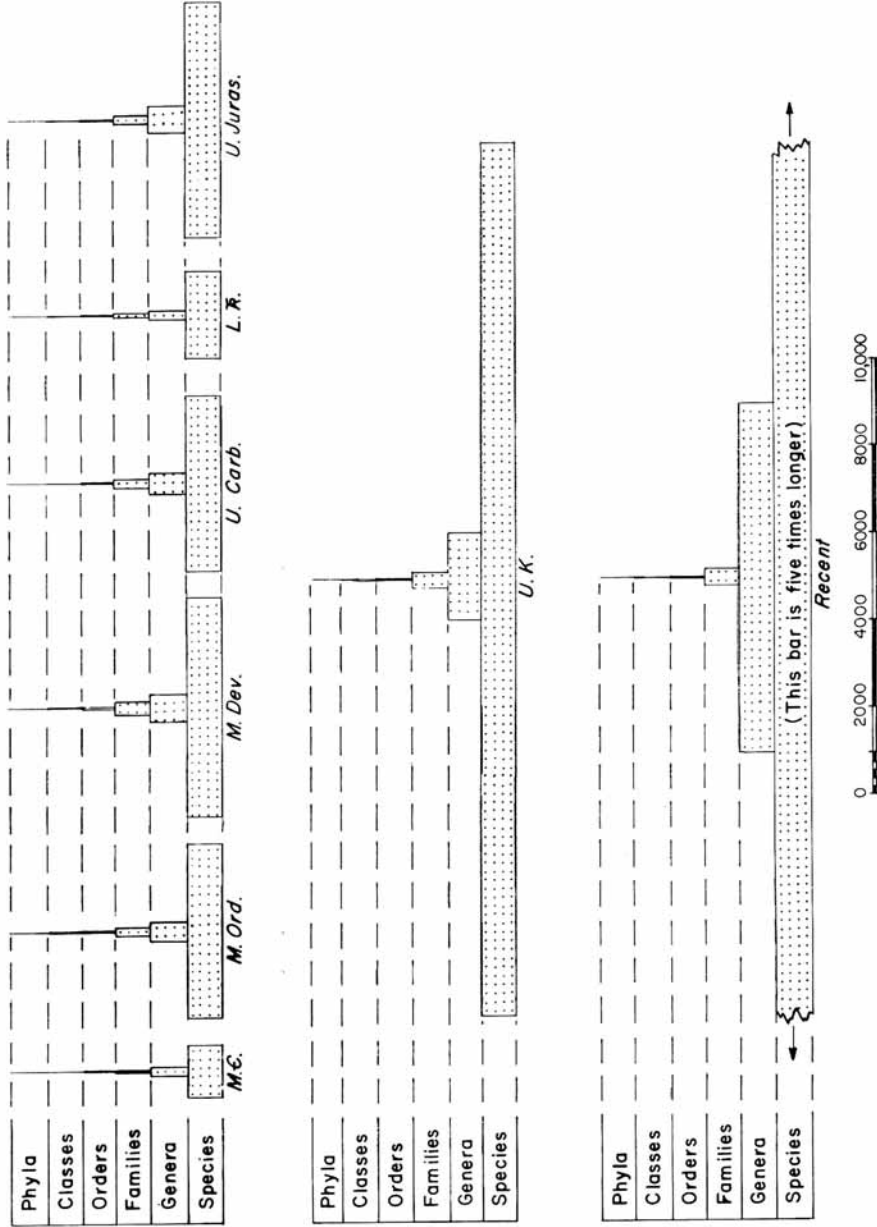
TEXT-FIG. 10. Approximate average standing diversities of the taxa of skeletonized shelf benthos included in the samples during various Series and at present. Diversities of familial and higher levels are based upon actual tallies. Diversities at generic and specific levels are calculated from scattered data on their proportions to families, except for the Recent. Recent generic and specific diversities are conservative estimates based on the literature.

would almost any additional taxon). At higher levels, they would raise ordinal diversity in medial Paleozoic and class diversity in early Paleozoic times, emphasizing graph patterns. Clearly, their exclusion does not affect the major diversity trends.

COADAPTATION OF ECOLOGICAL AND TAXONOMIC HIERARCHIES

The correlation of the structures of the two hierarchies under consideration is best approached at the species level. The fluctuations in species diversity, which have changed through a whole order of magnitude and more at times (Valentine 1967), naturally cause wide fluctuations in the numbers of populations in the ecological hierarchy, which must be accommodated in some manner.

In general there are three ways in which new species populations might be accommodated in ecological units (Klopfer 1962): (1) they may colonize parts of the environmental lattice that were previously unoccupied, in which case their niches represent an extension of ecospace in the ecological unit but average niche size is little affected; (2) space for their niches may be created in the lattice by shrinking one or several of the pre-existing niches, in which case the existing ecospace becomes more crowded by partitioning and average niche size decreases; or (3) parts of their niches may overlap with one or several pre-existing niches and thus crowd the lattice by overlap rather than by partitioning. The last sort of accommodation, by niche overlap, occurs hand in hand with one of the other sorts. The fitting of a new niche into the lattice may commonly involve all these sorts of accommodation. Theoretical or practical aspects of niche partitioning, which were touched on by Darwin (1859), have been considered in a modern perspective by a number of workers (for example, Bray 1958; Brown and Wilson 1956; Klopfer and MacArthur 1960, 1961; Klopfer 1962; McLaren 1963; MacArthur and Levins 1967; MacArthur and Wilson 1967; Hutchinson 1967; and Miller 1967). Yet data on variations in niche size and its relation to species diversity among marine shelf invertebrates is scanty. Marine research includes the work of Kohn (1959, 1966) on the gastropod *Conus* and Connell (1961) on some intertidal barnacles.

The most recent major rise inferred in species diversity from the late Cretaceous to the present seems to have involved an extension of ecospace, an invasion of parts of the lattice which were becoming newly realized, thus expanding the available environment. This increase in environmental heterogeneity in the shallow marine realm was evidently due partly to the cooling of shelf waters in high latitudes (Smith 1919; Durham 1950; Valentine 1967, 1968a), which permitted the rise of new biogeographic provinces in separate chains along north–south-trending coastlines. New provinces may also have been created by the drifting apart of some continents, progressively isolating, from about medial Cretaceous time, shelf regions that had previously been connected. This permitted an increase in endemism.

Thus this expansion of ecospace is envisaged as due primarily to two factors: (1) extension of the thermal factors and of numerous other parameters that are related to temperature, creating one set of biogeographic barriers; and (2) the creation of another set of barriers through the breaking up of formerly continuous or nearly continuous epicontinental seaways and continental shelves through continental drift (which in effect multiplies biospaces along dimensions of real space). The relative timing of these events is not yet clear, although there is a suggestion that longitudinal provinciality was

strengthening in the late Cretaceous (Sohl 1961) while latitudinal provinciality was still weak. The Cretaceous–Cenozoic expansion of ecospace was fundamentally on the level of the biosphere and involved the rise of provinciality, which in turn permitted new communities based upon endemic populations to appear in each province. The increase in isolation among the populations living in separate provinces or separate communities permitted the formation of many new species.

The increase in generic diversity follows from the multiplication of species and their isolation in separate provinces or communities. Different but related species with similar morphological adaptations would arise in similar habitats in different provinces, forming associations such as Thorson's (1957) parallel bottom communities or becoming 'geminate' or twin species such as occur on opposite sides of the Isthmus of Panama (Ekman 1953). The increase in generic diversity would be proportionately less than in species diversity, owing to the multiplication of similar morphological types in distinct provinces that would be grouped as genera by taxonomic practice. The same principle seems to apply to the family level. A marked increase in the diversity and provinciality of genera would lead to a more or less modest increase in family diversity. That the present biogeographic pattern of diversity is similar at the familial, generic, and specific levels has been well documented for the Bivalvia by Stehli, McAlester, and Helsley (1967). Kurtén (1967) suggested that mammalian diversity is high at the ordinal level because of endemism arising through the isolating effects of continental drift.

At higher taxonomic levels on the marine shelves a different factor must be operating to control diversity, since higher taxa do not much participate in the Mesozoic–Cenozoic diversification. Perhaps this diversification has occurred too recently for evolution to have proceeded to the level of higher taxa. The pattern of ordinal diversity suggests that this may be the case. Yet class diversity has declined since the Ordovician. A better explanation may be that the available biospace of the epicontinental seas and shelves was nearly fully occupied since at least very early in the Phanerozoic, and most increases in taxonomic diversity had to be accomplished by ecospace partitioning and overlap (see Rhodes 1962, pp. 270–2; Nicol 1966). Thus only in times of unusual expansion of the marine shelf biospace, when the realized parts of the environmental lattice increased persistently, would significant diversity increases result simply from the invasion of new biospace. Ecospace partitioning involves a decrease in the niche sizes of populations, at least along dimensions where competition may occur (Miller 1967), and this is not a process that lends itself to the appearance of organisms with wholly new ground-plans or with major modifications thereof, such as are required for the development of higher taxa. It is instead a process suited more to the modification in detail of pre-existing morphological types, so as to accommodate to smaller ecospaces—in other words, a process suited to the increase of specialization.

By Cambrian time or shortly thereafter the ground-plans that are the hallmarks of the major invertebrate phyla had been established. Most of the species were by present standards primitive and functionally generalized; modal niche size was no doubt far larger than at present, though there certainly may have been some highly specialized forms. Evidently, diversification in the Cambrian and Ordovician led to the presence in late Ordovician time of a large number of higher taxa. This may have been partly due to an expansion of biospace and should have included an increase in resources. As much of the former marine shelf biospace may have been occupied by soft-bodied organisms,

the expansion of skeletonized forms may have involved the appropriation of some resources that had formerly been utilized by soft-bodied groups. On the other hand, on the assumption that soft-bodied taxa should have responded to the same opportunities as skeletonized taxa, it seems even more likely that there was a concomitant diversification of soft-bodied lineages. These are debatable points, but it is clear that it cannot be assumed that Cambro–Ordovician radiation was occurring in vacant biospace. Vast regions of the lattice must have been occupied, and this may have served to channel the evolutionary pathways of diversifying lineages.

Certainly there was unusual extinction among higher taxa during this time. Higher taxa in the sample that appear in the Cambrian, but which are not known to have survived the Ordovician, include the phylum Archaeocyatha, the echinoderm classes Homostelea and Helicoplacoidea, the inarticulate brachiopod orders Obolellida, Paterinida, and Kutorginida, the monoplacophoran order Cambridoida, and the trilobite orders Redlichiida and Corynexochida. Numbers of other taxa that are poorly known also disappeared early, and may have represented higher taxonomic levels. They were not included in the sample because of their questionable status. These include some trilobitoids, some early echinoderm stocks, and early gastropod-like molluscan stocks. Perhaps most of these are functionally generalized forms, the morphological architecture of which proved unsuitable to the demands for specialization.

Biospace formerly occupied by populations of extinct lineages would soon be recolonized by populations of the lineages that remained, if such colonization did not actually precede and contribute to the extinction. This easily leads to the diversification of extant lower taxa, but not to the creation of taxa on a comparably high level. In the early Phanerozoic the large average size of the former ecospaces of extinct taxa provided ecological room, so to speak, which allowed the lineages that reoccupied vacated biospace a certain leeway for progressive morphological modification that could still lead to the establishment of a higher taxon. Later, when vacated biospace was to be in smaller parcels, opportunities for morphological modifications became limited, as during medial Paleozoic time, when the diversity of classes declined markedly (text-fig. 3). Although diversity of orders (text-fig. 3) and families (text-fig. 4) also declined during that time, the decline was less marked, and order/class and family/order ratios were both rising. This suggests that the extinction of a higher taxon was not usually accompanied by replacement at the level of the higher taxon but at a lower level. It also suggests that biospace was decreasing. In the Lower and Middle Permian the numbers of species and genera may well have been disproportionately higher than is suggested by the number of families, owing to the development of reef associations.

Towards the close of the Paleozoic the change in the taxonomic structure suggests a great reduction in the heterogeneity of the shelf environment. Provinciality was already low. It is not certain, therefore, whether a significant further reduction occurred or indeed was even possible in late Permian time. However the numbers of communities certainly decreased (for example, the late Paleozoic reefs disappear) and, although there are not well-documented field studies, it appears from faunal lists that the numbers of populations in the remaining communities also declined. Thus the ecological structure shrank at all, or nearly all, levels, suggesting a general decline in biospace. There are too few data on the ecological hierarchy of Permo-Triassic times, however, to support speculation on the precise causes of the extinctions on this basis. Rhodes (1967) has

reviewed the major hypotheses of extinction and remarks that probably none of them alone would cause the sorts of changes found at the Permo-Triassic boundary.

Rediversification evidently began by medial Triassic time, unless the increase in family diversity then is an artifact. If it is real (and it includes the beginnings of Scleractinian radiation as well as the expansion of gastropod families), it suggests that generic and specific diversification was proceeding at even higher rates. Presumably biospace had expanded (or was expanding) once more and the newly realized parts of the environmental lattice were being recolonized. However, compared with Cambro–Ordovician lineages, Triassic lineages were rather specialized, with smaller modal niche sizes, so that the average colonizing lineage must have occupied a relatively smaller part of the lattice. The opportunities now presented for the formation of higher taxa could not be much exploited by the relatively specialized populations. There may be exceptions; the Scleractinia may have taken advantage of biospace vacated by Paleozoic coelenterate lineages to become skeletonized and reoccupy some of the same biospace. Finally, at some time in the Mesozoic a diversification involving the marked rise in provinciality discussed previously began to occur as well. It seems likely that the Jurassic and early Cretaceous diversity increases, which are not inconsiderable and which take place at a high rate (text-fig. 5), are partly owing to an increase of latitudinal provinciality due to cooling poles and to an increase of longitudinal provinciality due to the separation of some continental masses in Jurassic time. A thorough analysis of the biogeographic patterns of Mesozoic diversification is badly needed.

The Cretaceous–Cenozoic boundary is marked by extinctions of some benthonic marine groups (see Hancock 1967), but if there was any appreciable alteration in the taxonomic diversity structure at the family and higher levels it was of so short a duration that it does not appear in the present data. The structure of communities, provinces and of the entire shelf realm must have undergone qualitative changes, but this is a more or less continuous process on the broad scale we are considering. The Late Cretaceous rise in diversity extends unabated across the Cretaceous–Cenozoic boundary. Surely there was no large-scale reduction in biospace.

Two major modes of taxonomic diversification have been described, both proceeding at progressively lower taxonomic levels through time. The first involves a biospace that fluctuates about some size that does not vary much in time. Diversification at the population level at first proceeds by colonization of untenanted biospace, but soon must be accompanied by a progressive decrease in average niche size. Communities therefore become increasingly packed with more and more specialized populations and begin to fragment into portions, each of which has an energy flow that is partially independent of the others. The isolation and independence of these portions will increase with further specialization until they form ecosystems that are as independent as the original one from which they fragmented. Slighter and slighter environmental discontinuities will form community boundaries until the environmental mosaic of a given primitive community, relatively heterogeneous but occupied by primitive populations with large niches, is broken up into a number of smaller environments, each more homogeneous than the original and each occupied by more specialized populations. Provinces become packed with more and more communities that have progressively smaller ecospaces. The diversity of provinces is not so sensitive to this progressive specialization, although it may eventually be affected if the trend continues long enough. Any widespread partitioning

of temperature or temperature-correlated parameters would lead to increased provinciality even in the absence of progressive changes in the latitudinal temperature gradient. If partitioning were to continue, smaller and smaller changes in thermal regimes would act to localize range end-points, and thus form provincial boundaries (Valentine 1966). In sum, in this mode the ecological structure evolves from lower levels towards higher.

The other mode of diversification involves a biospace that expands to create new environments or to add new dimensions (or at least to extend old dimensions) to old environments. New environments may be created, for example, through climatic changes, and old environments may be extended through the improvement of limiting factors, that is through the amelioration of conditions which tended to inhibit diversification.

From what is known and can be inferred of the hierarchies of the Paleozoic, diversification (at least after an initial radiation of skeletonized taxa and probably before) was proceeding chiefly in the first mode, from the bottom of the ecological hierarchy upwards, implying a relatively stable biospace. Rediversification following the Permo-Triassic extinction was probably in the second mode, involving an amelioration of factors that had inhibited diversification, and the Upper Cretaceous and Cenozoic diversification seems to have also been in the second mode, but involved the creation of new environments. Nevertheless there must have been continuing specialization and thus the first mode was also active in the taxonomic and ecological evolution, Processes that bring species that appeared during biospace expansion into sympatry with older lineages, such as 'species pumps' of various kinds (Valentine 1967, 1968a), may link these two modes into a single system of diversification. Finally, the more lineages that exist the greater the opportunity for large-scale diversification under appropriate circumstances in either mode. This factor is certainly at work in the disproportionate multiplication of lower taxa during Cretaceous and Cenozoic times.

A number of authors have suggested that extensive changes in sea level may control some of the diversification and extinction patterns (Newell 1952, 1956, 1963; Moore 1954; see Rhodes 1967 for other references). Widespread epicontinental seas, it is asserted, provide more inhabitable area for shelf invertebrates and therefore more opportunity for diversification, while regressions reduce the inhabitable area and thus the diversity. There is some theoretical support for this position in the species-area work of Preston (1962), Williams (1964), MacArthur and Wilson (1967), and others. Little work has been done in marine environments; the areas of ancient shelf seas, especially during regressive phases, are difficult to estimate (though see Ronov 1968); and the effects that could be expected in a biosphere of vastly different ecological and taxonomic structure and composition are largely uncertain. The problem is further complicated by facies differences between epicontinental seas and shelves bordered by open oceans. Although uncertainties in calculations must be great, preliminary estimates suggest that the species-area effect would have been far too small to account for major diversifications and extinctions by itself. Moreover, we live at present in a time of great continental emergence yet the shelves are richly diverse in lower taxa and in ecological units at all levels, precisely the opposite of the pattern of Permo-Triassic extinction. Indeed, a relative lowering of sea level must commonly result in the emergence of land barriers which isolate regions formerly connected and permit the rise of an endemic biota in each region. This would have the effect of increasing the total number of species in these regions.

Nevertheless, the elimination or rise of species resulting from shelf-area fluctuations would certainly contribute to diversity patterns, and further evaluation of this subject is clearly merited.

CONCLUSIONS: THE PROGRESSIVE CANALIZATION OF ECOSPACE

It is concluded that a major Phanerozoic trend among the invertebrate biota of the world's shelf and epicontinental seas has been towards more and more numerous units at all levels of the ecological hierarchy. This has been achieved partly by the progressive partitioning of ecospace into smaller functional regions, and partly by the invasion of previously unoccupied biospace. At the same time, the expansion and contraction of available environments has controlled strong but secondary trends of diversity. Present marine biospace is in fact unusually extensive, and the world's shelf seas are therefore unusually heterogeneous and support a large number of ecological units today. The relations of these trends to trends within the taxonomic structure of the benthonic invertebrates are intimate.

Assuming for the moment that evolutionary trends among marine benthonic invertebrates will continue and that biospace does not change much (a dim prospect in view of rising pollution), what might be predicted of the future structures of the ecological and taxonomic hierarchies? Speculation on this point may be of some value to underline the sort of process that is postulated to have gone before. Clearly, the trend towards specialization would further reduce the average niche sizes of species. It would be increasingly difficult for evolving lineages to depart much from their modal functions and morphologies, as biospace would become available only in increasingly smaller compartments. The amount of change necessary to produce a new family would be increasingly difficult to attain, and eventually no new families could appear. In fact, some families would become extinct so that familial diversity would decrease, and lineages from other families would fill any vacated biospace. After some time genera could no longer appear, for biospace would be packed too tightly to permit morphological variation even at that level, and generic diversity would decline for a while as some extinction, inevitably, occurred. Eventually, all the biospace would become filled with evolving lineages with an incredibly small modal niche size, each lineage constrained by the presence of all the others to evolve in only a narrow pathway directed by the trends of evolution of the entire biota, and of changes in the entire biosphere. Ecological units are now exceedingly small by today's standards, with virtually every few food-chains forming a separate community and every moderate topographic irregularity forming a provincial boundary. Canalization of ecospace is complete. The biosphere has become a splitter's paradise.

Although this extrapolation cannot be taken too seriously, it does point to some important consequences of ecospace partitioning. First, average species of the early Paleozoic, with their broad niches, may have had different patterns of morphological variation than the specialized species of today. Secondly, the occurrence in the early Paleozoic of numbers of unusual 'aberrant' higher taxa that contain few lower taxa is not necessarily due to a poor fossil record but is probably the natural consequence of adaptive strategies that prevailed in primitive ecosystems of low diversity. Finally, extinction of taxa of high diversity is less likely than extinction of taxa of low diversity, other

things being equal (Simpson 1953), simply because so many more lineages must disappear. Similarly, the markedly rising provinciality of the late Cretaceous and Cenozoic will tend to make the extinction of the newly diverse taxa that have representation in many provinces—a common situation even on the generic level—more difficult.

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