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Introduction

Antonie van Leeuwenhoek, the incomparable pioneer microscopist of Delft, examined some dissected shrimps and wrote the following in 1700, in one of his famous letters:

"In some of their stomachs, I also discovered very little snail-shells, which, because of their roundness, I called little cockles; and these little shells were no bigger than a coarse sand-grain. In order to exhibit the pretty structure of these little shells before the eye, I thought it would not be amiss to get a drawing made of one of them." (Dobell, 1932.)

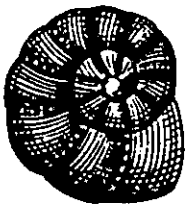

Figure 1. Leeuwenhoek's "little cockle."

The drawing (fig. 1) is of a benthic foraminifer, apparently an Elphidium. Leeuwenhoek was unaware that microscopic foraminifera had been illustrated by at least two other previous observers, Ulisse Aldrovandi and Robert Hooke (Pokorny, 1963). Thus, about 4 genera of smaller benthic foraminifera were known at the beginning of the 18th century. The number increased to about 60 by 1835 when the foraminifera were recognized to be protists by Felix Dujardin, and to about 1200 by 1964 when the authors of the most widely used present classification of the group described all genera they considered valid (Loeblich and Tappan, 1964). In all, about 3000 generic names have been proposed in the past 200 years, about half of them synonyms (Loeblich and Tappan, 1974).

The foraminifera constitute an "order" with both benthic and planktonic adaptations. The vast majority of foraminiferal taxa, however, are benthic. They include all tectinous, agglutinated, calcareous microgranular, and calcareous porcelaneous forms. Among calcareous hyaline foraminifera, 11 out of 12 superfamilies in Loeblich and Tappan's revised classification (1974) are benthic. Consequently, in terms of morphological variation and spatial and temporal distribution, benthic foraminifera constitute the most thoroughly studied group of microfossils.

This lecture deals mainly with patterns of distribution of modern benthic foraminifera and their significance in paleoenvironmental analysis. Most of the widely distributed families of modern benthic foraminifera have a fossil record dating back to Paleocene or earlier times. A partial list of such families (Loeblich and Tappan, 1964, 1974) is given below.

Agglutinated: Ammodiscidae, Ataxophragmiidae, Astrorhizidae, Hormosinidae, Lituolidae, Saccamminidae, Textulariidae, Trochamminidae.

Porcelaneous: Fischerinidae, Miliolidae, Nuebeculariidae, Soritidae.

Hyaline: Alabaminidae, Anomalinidae, Asterigerinidae, Bolivinitidae, Buliminidae, Calcarinidae, Cassidulinidae, Caucasinidae, Ceratobuliminidae, Cibicididae, Cymbaloporidae, Discorbidae, Elphidiidae, Eponididae, Gladulinidae, Islandiellidae, Nodosariidae, Nonionidae, Osangulariidae, Polymorphinidae, Robertinidae, Rotaliidae, Spirillinidae, Turrilinidae, Uvigerinidae.

Among modern calcareous or agglutinated foraminifera, there are only 4 minor families, each represented by 1 genus, that have no fossil record.

Species diversity

The simplest measure or index of faunal diversity is the number of species in the assemblage. An inshore to offshore increase in the number

of benthic foraminiferal species has been reported from several continental shelves. For example, Walton (1964) reported that in the northeastern Gulf of Mexico, all faunas with less than 20 species are present in depths less than 18m, whereas those with more than 81 species are present in depths greater than 91m, a more less steady increase being observed in intermediate depths. On the Sunda Shelf, 3 species exist at the shoreline and 107 at the outer edge (Biswas, 1976). Betjeman (1969) reported a general increase in the number of species with depth on the western Australian shelf; diversity peaks were found at 91m and 238m but a pronounced decrease was observed near the shelf-edge.

A variety of diversity indices has been used in which the relative proportions of the constituent species of an assemblage are taken into account. The Yule-Simpson index (Simpson, 1949) is given by $\frac{N\ (N-1)}{\sum_{i=1}^{s} n_i\ (n_i-1)}$, where N is the total number of individuals, n_i is the number of individuals of the ith species, and s is the number of species. The value of this index shows a progressive increase off the North Carolina coast, from less than 10 on the inner shelf to more than 30 on the outer shelf (Schnitker, 1971).

A widely used index based on the information theory, the Shannon-Wiener function, is given by $-\sum_{i=1}^{s} p_i \ln p_i$, where p_i is the proportion of the ith species in the sample. The function is much less dependent on the size of the sample than either the simple species diversity (s) or the Yule-Simpson index. On the Atlantic continental shelf of North America, the Shannon-Wiener function generally shows an increase with increasing depth (Gibson and Buzas, 1973). However, on the southern part of this shelf, off the coast of Georgia, the value of the function rises from the shoreline to water depths of about 15m, and then remains steady with values close to 3. The simple species diversity shows a compatible change, with values close to

50 being typical of the middle and the outer parts of the shelf (Sen Gupta and Kilbourne, 1974).

The increase in the values of diversity indices in deeper waters is commonly explained by the time-stability hypothesis (Sanders, 1969), the "stability" of the environment increasing and the "unpredictability" decreasing from the shoreline to the shelf-edge and beyond. There may, however, be areas on the shelf where the environmental stability, in terms of persistence of physical, chemical, or biological factors, does not show much variation, and thus the diversity values do not show any perceptible gradient (Sen Gupta and Kilbourne, 1974). Even when the values of species diversity rise from the shoreline to the shelf-edge, the gradient is gentle and may not help in delineating depth zone boundaries. One exception may be the inshore-offshore boundary, usually close to the 15 or 20m isobath, at which the slope of the diversity curve may show a change.

Depth zones based on distribution trends of species

Example: Pacific continental shelf of North America

For almost 50 years, depth zones or "biofacies" have been recognized on various continental shelves and slopes on the basis of occurrences of chosen stenobathic species (see Sen Gupta, 1977, for review). The classic area where this approach has been used by many workers is the Pacific continental margin of North America. The earliest of the foraminiferal depth-distribution studies in this region was by Natland (1933) who recognized "five distinct faunal assemblages in close proximity" in the channel between Long Beach and Santa Catalina Island, California. These assemblages were regarded as constituting "faunal- or life-zones" with characteristic bottom-water temperatures and depths. The 3 zones in the shallower part of the channel and their abundant species were as follows:

Zone I - nearshore, brackish-water lagoon: Ammonia beccarii;
Zone II - depth range 4-40m: Nonion scapha and Elphidium articulatum;
Zone III - depth range 40-275m: species of Cassidulina. In the same general area, McGlasson (1959), using relative abundances of benthic foraminiferal species, identified 3 depth zones (approximately, 0-40, 40-80, and 80-200+m) around Santa Catalina Island. The compositions of living and dead assemblages were found to be "essentially different" in each of these zones.

Foraminiferal zonation along the North American Pacific coast has generally been based on shallow and deep limits of selected species and on species frequencies or relative abundances (Phleger, 1965). A nearshore, turbulent zone was recognized in most studies. However, conspicuous differences can be observed in the exact locations of zone boundaries in the regional or local schemes proposed by different workers.

The use of the bathymetric ranges of stenobathic species in the recognitition of depth zones in the eastern Pacific is illustrated well in Phleger's (1965) study of Gulf of California assemblages. Fig. 2 shows part of Phleger's species-distribution chart, for depths above 200m, and includes only the abundant or common species. The 25m boundary was actually recognized by the shallow limits of 13 species and by the deep limits of 2 species, viz., Ammonia beccarii and Rosalina columbiense. The 35 m, 75-85m, 120m and 180m boundaries were recognized by the shallow limits of 8, 8, 1, and 3 species, and by the deep limits of 3, 7, 6, and 17 species, respectively; the shallow limits of 2 species characterized the 55m boundary.

Example: Northern Gulf of Mexico

Numerous reports have been published in the past 30 years on the benthic foraminiferal zonation in northern Gulf of Mexico. The following partial summary of zone-indicator assemblages has been adapted from

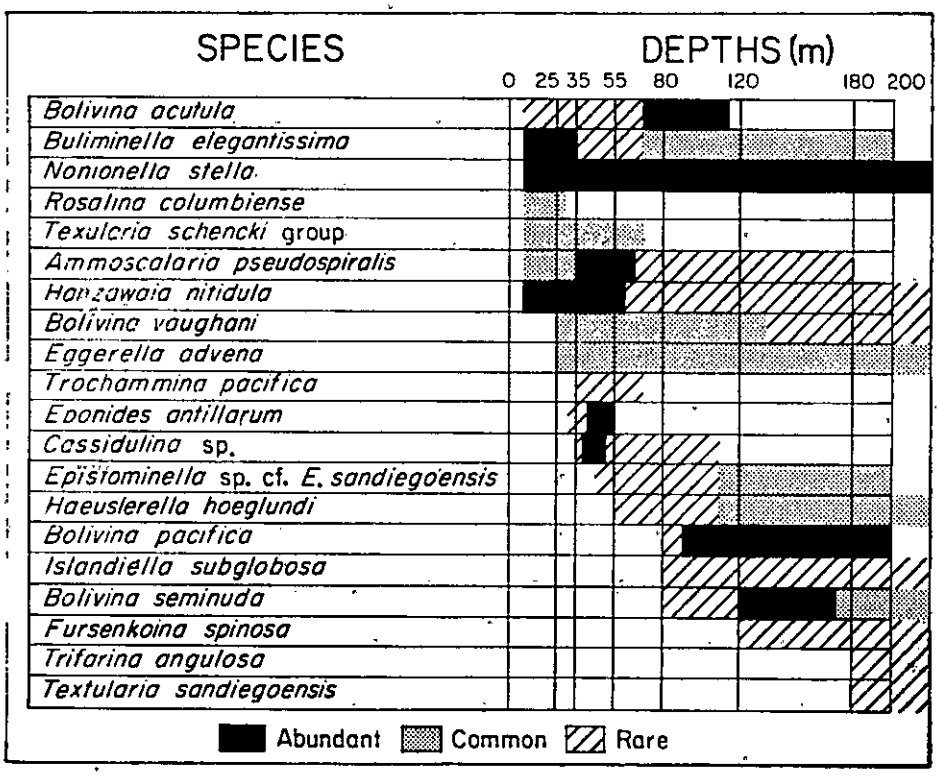

Figure 2. Depth ranges of living populations of selected species in eastern Gulf of California, 0-200m. Foraminiferal zone boundaries have been recognized at depths of 25, 35, 55, 75-85, 120, and 180m. Adapted from Phleger (1965).

Albers et al. (1966, for neritic species) and Pflum and Frerichs (1976, for bathyal and abyssal species). The depth limits of the zones are approximate.

A. NERITIC: (i) Inner neritic (0-20 m): Miliolids, Hanzawaia strattoni, Ammonia beccarii, Nonion grateloupi, Bigenerina irregularis, Elphidium spp.

(ii) Middle neritic (20-100 m): Amphistegina lessonii, Cristellaria subaculeata, Eponides antillarum, Siphonina pulchra, Marginulina planata, Bolivina striatula.

(iii) Outer neritic (100-200 m): Bulimina marginata, Bolivina subaenariensis, Globobulimina pacifica, Gaudryina atlantica, Cassidulina subglobosa, Cibicides floridanus (large).

B. BATHYAL: (i) Upper bathyal (200-500 m): Bolivina albatrossi, Bulimina inflata mexicana, Chilostomella oolina, Uvigerina peregrina, Bulimina aculeata, Gyroidina orbicularis.

(ii) Middle bathyal (500-1000 m): Cyclammina cancellata, Cibicides kullenbergi, Cibicides rugosus, Oridorsalis tener umbonatus, Osangularia culter.

(iii) Lower bathyal (1000-2000 m): Anomalina globulosa, Siphotextularia rolshauseni, Uvigerina ampullacea.

C. ABYSSAL (> 2000 m): Uvigerina senticosa, Melonis pompilioides.

Biogeographic limits of stenobathic species

Most depth-restricted species of continental shelves also exhibit strong geographic restrictions. A survey of known distribution patterns of benthic foraminifera led Phleger (1960) to draw only 2 conclusions about general depth limits of very widely distributed species. (1) Depths less than 70-100 m are characterized by Buliminella elegantissima, Ammonia beccarii, some species of Rosalina, some species of Eggerella,

species of Elphidium, and abundant miliolids, including Quinqueloculina seminulum. (2) Depths greater than 100 m are characterized by Hoeglundina elegans and Uvigerina peregrina. These conclusions have been supported by studies done in many areas since the publication of Phleger's book.

If the perspective is narrowed from the entire World Ocean to a region consisting of several biogeographic provinces, many species are found to be characterized by rather limited depth ranges. For instance, a shallow water or inner shelf zone, confined between the shoreline and an isobath of 15-20 m, is easily recognized along much of the Atlantic coast of North America on the basis of a relative abundance of Elphidium excavatum forma clavatum and Ammonia beccarii. In fact, an Elphidium-Ammonia assemblage, with or without the two particular species mentioned above, seems to characterize the nearshore turbulent zone on most continental shelves of the World Ocean. Special habitats, such as reefs, vegetation, or rocky bottoms, may, however, support special faunas (Sen Gupta and Schafer, 1973).

The dominance of Elphidium excavatum forma clavatum in shallow water assemblages of a high northern latitude belt was documented Smith (1970). The southern boundary of the belt occurs near the latitudes of northern Washington and northern Japan and Korea in the Pacific, off England and northern Germany in the eastern North Atlantic, and between Cape Cod and Maryland in the Western North Atlantic. This faunal province is best developed in waters shallower than 30 m, with E. excavatum f. clavatum reaching its maximum abundance in depths less than 15 m. Great variations of salinity (15‰ to 35‰) and temperature (annual range almost 0 to 25°C) are recorded within the province.

Few common dominants have been recognized in deeper parts of continental shelves that span multiple biogeographic provinces. However,

in many areas, middle shelf assemblages of tropical and subtropical waters, inhabiting depths near 50 m, are dominated by species of Hanzawaia, including H. concentrica. Bulimina marginata and Uvigerina peregrina, typical forms of the bathyal environment, dominate many shelf-edge assemblages.

In general, precise depth limits of stenobathic species show considerable variation in different areas because of the variation in bottom-water conditions. If cumulative depth ranges are considered for entire geographic distributions of these species, most of them would appear eurybathic; the problem is compounded when the depth data are based wholly or partially on dead populations. A graphic representation of overall depth limits of all reported species from an extensive region, such as the continental shelf and slope off the eastern United States (McLean, 1971), does not help much in identifying the foraminiferal zones that may exist.

Zonation by numerical techniques

Numerical techniques of data analysis have been employed by several recent workers for recognition or comparison of foraminiferal facies on continental shelves. Buzas (1970) briefly reviewed many of these studies; the commonly used techniques are explained in Sneath and Sokal (1973). A few examples are discussed below.

Buzas (1967) examined Phleger's (1956) data on foraminiferal abundances along the central Texas coast of the Gulf of Mexico and applied the technique of canonical variate analysis (Seal, 1964; Blackith and Reyment, 1971) to compare faunal areas. These areas were chosen because of "consideration of geography, distribution of traverses, and Phleger's suggested faunal boundaries." They were compared on the basis of mean vectors of abundances of 45 species that were present in both living and total populations. In the total assemblage, 94% of the variability was due to the first 3 canonical variates.

On the open shelf, 3 areas between 0 and 30 m were recognized as similar; 2 other areas, between 30 and 60m, and between 60 and 110m, were recognized as discrete. The depth boundaries of these biofacies generally agree to those originally suggested by Phleger (1956). The living assemblage of one of the 0-30 m areas, however, was recognized as distinct from the other two.

Streeter (1964) demonstrated by vector analysis that 7 assemblages account for 85% of the variability present in Drooger and Kaasschieter's (1958) foraminiferal data for the Orinoco-Trinidad-Paria shelf. The thanatotopes characterized by these assemblages are more or less the same as those identified by Drooger and Kaasschieter on the basis of species abundances; they are apparently related to the depth gradient on the shelf.

Schnitker (1969) used factor analysis to distinguish thanatocoenoses on the outer shelf of Bay of Biscay, between depths of 110 and 145 m. Four factors (species groups) accounted for about 97% of the total variability: Schnitker observed that 3 of the thanatocoenoses show a relationship to the distance from the shore; the fourth is present on some elevated areas.

The diverse techniques of cluster analysis (Sneath and Sokal, 1973; Everitt, 1974) have helped in the grouping of samples in several areas. Both R-mode (comparison of species for samples) and Q-mode (comparison of samples for species) analysis have been employed. Three parts of the western North Atlantic continental shelf, 2 north of the Cape Hatteras biogeographic barrier and 1 south of it, provide good illustrations.

Kafescioglu (1975) recognized several thanatotopes on the Massachusetts shelf and upper slope, using presence-absence data for species and for genera. He concluded that a Q-mode unweighted-pair analysis of the Jaccard coefficients (given by $p/(p+m)$, where p = number of positive matches and

m = number of mismatches) at the generic level gave the best results. Three large clusters obtained by this method represented a "shallow-water" (0-50), an "upper shelf" (50-100m), and a "lower shelf/upper slope" (deeper than 100m) thanatotope.

The Sorensen coefficient of similarity is given by 2w/ (a+b), where w is the sum of the smaller values for all paired characters in 2 samples, a is the sum of all values in the first sample, and b is the sum of all values in the second sample. In a study of the benthic foraminifera of the Long Island continental shelf and upper slope, New York, Gervitz et al. (1971) calculated this coefficient for every sample pair on the basis of species percentages and then performed a Q-mode cluster analysis. They identified 11 distinct clusters at a high level of similarity. Three of these are located on the inner shelf, 4 on the middle shelf, 2 on the outer shelf, and 2 on the slope. The depth boundaries were recognized at approximately 35m, 75m, and 100m (shelf edge).

Sen Gupta and Kilbourne (1976) used the simple distance function (Parks, 1966) to measure the dissimilarity between samples on the Georgia continental shelf and slope. This function is given by

$$D_{1,2} = \left[\sum_{i=1}^{M} (Xi_1 - Xi_2)^2 / M\right]^{\frac{1}{2}}$$

where M is the number of variables and X is the normalized value of variables. The procedure of data analysis consisted of a number of steps, summarized below.

Frequency data on the 80 most widespread species were taken and an R-mode principal components analysis was performed on the matrix of the complement of the simple distance function ($1-D_{1,2}$). Three principal components accounted for more than 80% of the total variance. The original raw variables (species frequencies) were transformed into uncorrelated or

orthogonal variables by the computation of factor scores or component measurements for each sample. Finally, a Q-mode cluster analysis was performed on a simple distance function matrix by the unweighted pair-group method using arithmetic averages (Sneath and Sokal, 1973).

The resulting dendrogram (Fig. 3) exhibits 8 clusters at the 0.20 phenon level; of these, only 3 (A, C, and E) are major. On a station location map (Fig. 4), these 3 clusters correspond to distinct areas or thanatotopes with the following faunal characters:

Thanatotope 1 - abundance of Ammonia beccarii (inshore part), Planulina exorna, Planorbulina mediterranesis, and Elphidium excavatum forma clavatum; common occurrence of Quinqueloculina lamarckiana, Asterigerina carinata (deeper part), and Placopsilina bradyi (deeper part).

Thanatotope 2 - abundance of Planulina exorna, Planorbulina mediterranensis, Asterigerina carinata, and Quinqueloculina lamarckiana; common occurrence of Rosalina floridana and Elphidium excavatum forma clavatum.

Thanatotope 3 - maximum abundance of Planulina exorna, abundance of Cassidulina subglobosa, Textularia conica, and Bigenerina irregularis; common occurrence of Hanzawaia concentrica. The outer boundaries of thanatotopes 1 and 2 are close to the 25m and 40m isobaths, respectively. Thanatotope 3 comprises the area around the shelf-edge (depth about 50m). The inshore-offshore demarcation indicated by diversity changes, mentioned earlier, does not coincide with any of these boundaries; it lies within thanatotope 1.

The technique of recurrent group analysis (Fager, 1957) has been demonstrated to be useful in ecological interpretations of foraminiferal assemblages (Sen Gupta and Hayes, 1979). A recurrent group is defined as the largest set of species in the collection in which all of the

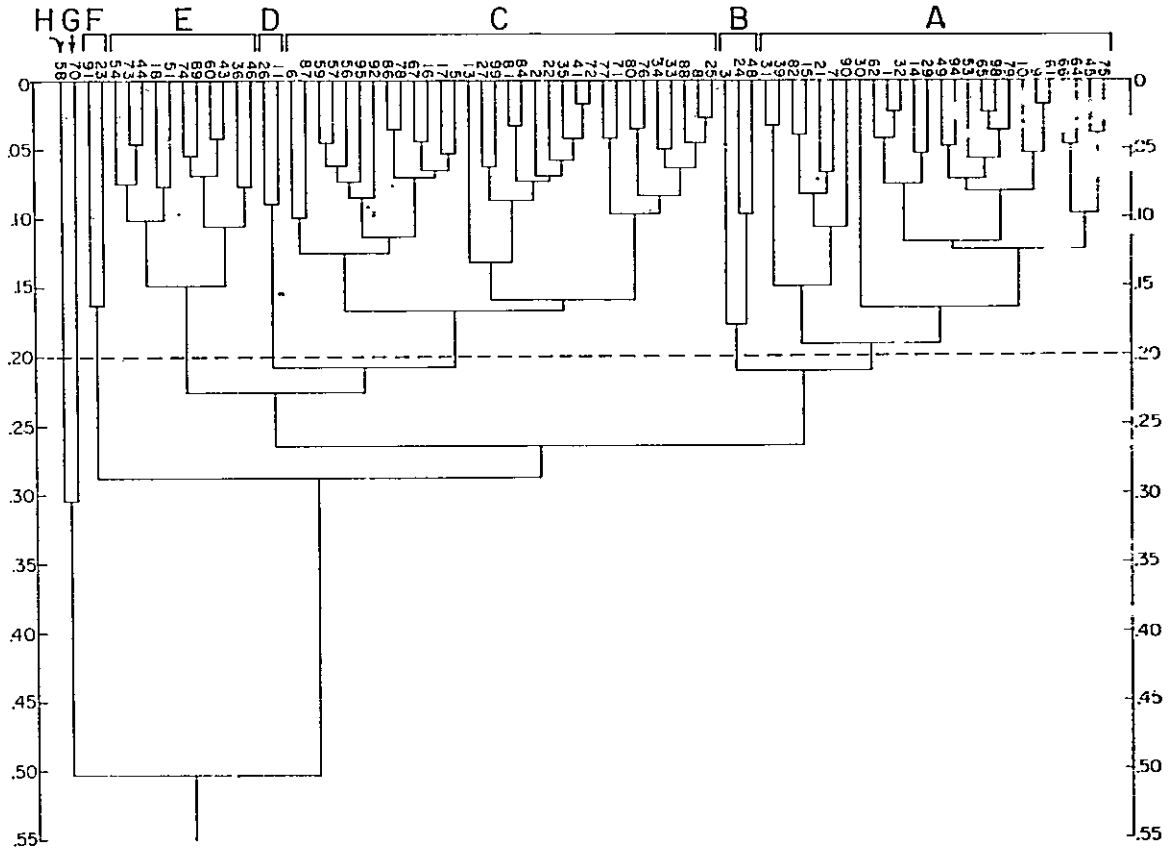

Figure 3. Q-mode dendrogram, derived by cluster analysis of foraminiferal abundance data from Georgia shelf and upper slope. The 0.20 phenon level is indicated by the dashed line; the clusters at this level are labeled A through H. From Sen Gupta and Kilbourne (1976).

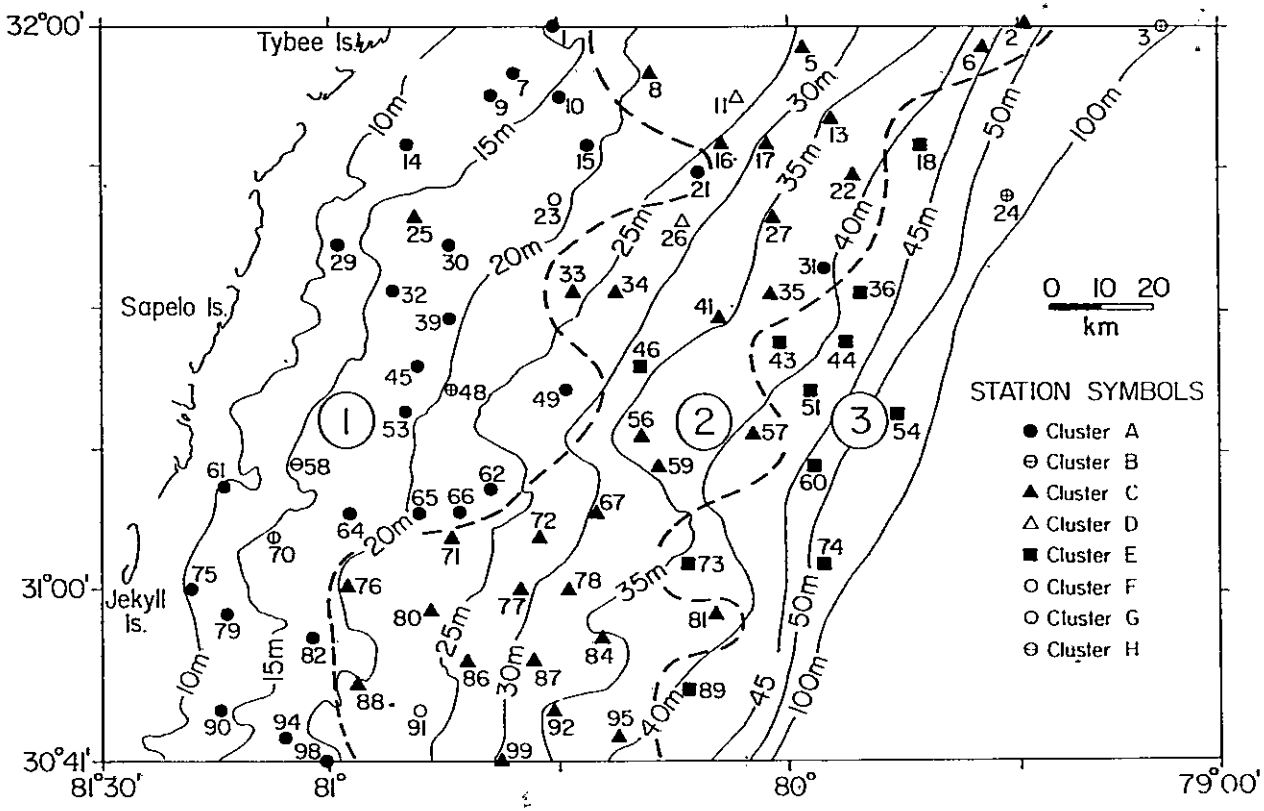

Figure 4. Georgia continental shelf and upper slope: Cluster affinities of stations. Thanatotopes are indicated by circled numerals and dashed boundaries. From Sen Gupta and Kilbourne (1976).

members show a significant degree of co-occurrence with all other members of the group. Once a group is identified from the data set, it is removed, and the next-largest recurrent group is found; this process continues until no further groups can be formed. The question of whether two species are significantly associated, over the range of sampling sites at which they occur, is resolved by the calculation of an affinity index, α. The affinity index between any two species, 1 and 2, is calculated from the formula:

$$\frac{a}{\sqrt{(a+b)\ (a+c)}} - \frac{1}{2\sqrt{\max[(a+b),\ (a+c)]}},$$

using the notation for a 2x2 contingency table, where:

a = number of samples in which species 1 and 2 occur together;

b = number of samples in which species 2 occurs but species 1 does not; and

c = number of samples in which species 1 occurs but species 2 does not.

In the standard procedure for recurrent group analysis, affinity indices are calculated with the above equation for all possible pairs of species in the collection (all sampling sites). Each of these indices is then compared with a predetermined threshold value for α; indices below the threshold are assumed to be non-significant (due to random chance), whereas indices above the threshold are assumed to represent a biologically caused association. It is from the pool of significant associations that the recurrent groups are formed.

Except for one significant difference, the results of recurrent group analysis of Georgia shelf foraminiferal data (Sen Gupta and Hayes, 1979) agreed with those of the Q-mode cluster analysis, discussed earlier. The recurrent group analysis indicated a thanatotopic boundary at about

15m of water depth (where the diversity curve attains a plateau); the cluster analysis did not reveal this boundary, but suggested a transition between two thanatotopes near the 25m isobath. Recurrent group analysis of benthic foraminiferal data from the Grand Banks of Newfoundland (Sen Gupta and Hayes, 1979) led to the identification of features of depth distribution not recognized earlier (Sen Gupta, 1971) by a study of the nume ical data on species frequencies; some possible substrate preferences were also identified.

Finally, a novel approach to bathymetric zonation using modern benthic foraminiferal frequency data has been recently proposed by Pielou (1979). The technique, called "precedence analysis", identifies species that are particularly sensitive to a chosen environmental factor and then places such species in "optimum indicator groups". In contrast to cluster analysis, the method utilizes only a "subset" of the species assemblage. Its usefulness lies in the recognition of trends of species distribution with regard to one selected environmental gradient, such as that of depth.

Paleoenvironmental studies

Most Cenozoic (particularly, post-Oligocene) fossil foraminiferal assemblages contain many extant species. Comparison of such assemblages with Holocene ones has led to the recognition of some overall characters of past depositional environments. Estimation of bathymetric limits of Tertiary sediments has been made in diverse areas on the basis of the composition of benthic formainiferal faunas. Some of the work has been reviewed by Vella (1962), Skinner and Eppert (1966), Funnell (1967), and Boltovskoy and Wright (1976). Some American studies are briefly summarized below.

In his classic analysis of foraminiferal facies in modern sediments off California and in a nearby stratigraphic sequence, Natland (1933) compared the assemblages present in the channel between Long Beach and Santa Catalina Island with Pliocene and Pleistocene faunas from Hall Canyon, near Ventura. He associated the Hall Canyon stratigraphic units with environments of deposition ranging from lagoonal to open-oceanic. The presence of certain species in the section also indicated a warming of water from the earlier to the later phase of deposition. Bandy and Arnal (1960) used the criteria of species diversity, richness of populations, abundances of porcelaneous, agglutinated, and planktonic species, and occurrences of particular extant species and their extinct "homeomorphs" to estimate the depths of sedimentation of middle Tertiary strata of San Joaquin Valley, California. The changes in paleobathymetry from one stratigraphic stage to another enabled them to calculate the "vertical component of tectonic movements which have affected the floor of the basin from one stage to another". The quantitative "geohistory analysis" proposed by van Hinte (1978) is partly based on estimates of subsidence by a paleobathymetric interpretation of the benthic microfossil record.

Gibson (1967) made a paleobathymetric analysis of a number of local stratigraphic units in North Carolina constituting the Pungo River and Yorktown Formations (originally reported as Miocene, now regarded as Miocene and Pliocene; Akers, 1972). The characters used were the frequency variations of species with known depth preferences in the modern North American Atlantic and the variation in the planktonic-benthic ratio. Gibson concluded that these characters indicated a progressive shoaling of the environment from more than 100m to about 15m and a warming of the water during the deposition of the younger beds. In a paleoecological study of

Paleocene stratigraphic units of the Atlantic Coastal Plain, Youssefnia (1978) used low benthic foraminifer diversity as a feature that distinguished "marginal marine" and "inner-neritic" environments from "mid-neritic" ones.

In the Gulf Coast region of the U.S., vertical and horizontal distributions of fossil benthic foraminifera have been extensively studied by academic and industrial paleontologists. The first reported micropaleontological investigation of subsurface samples from this area dates back to 1878; the samples were from a New Orleans well (Stuckey, 1978). Virtually all of the early work was solely for the purpose of biostratigraphic correlation. Beginning in the 1950's, however, a substantial number of studies were made in which the benthic foraminifera were used for charting time-transgressive facies and interpreting paleoenvironments. In connection with petroleum exploration, benthic foraminifera have been particularly useful in the recognition of suitable paleoenvironments in the Oligocene and Miocene clastic sediments of Texas and Louisiana (Tipsword et al., 1966). The well-studied modern distribution patterns of the Gulf of Mexico formainifera have aided immensely in these paleoenvironment reconstructions.

Making a judicious use of both extant and extinct species, Gernant and Kesling (1966) were able to recognize 7 depositional environments for the Oligocene Middle Frio sediments of southeastern Texas; these environments were "continental, brackish, saline bay, shallow inner shelf, deep inner shelf, middle shelf, and outer shelf." In subsurface sections of another Oligocene unit of Texas, the Anahuac Shale, Walton (1964) recognized marine depositional environments with depths ranging from less than 100 m to greater than 200 m, mainly on the evidence of dominant genera; one transgressive and one regressive sequence were discriminated. In the thick Miocene section of southern Louisiana, the transition

between the shelf and the slope facies, often of economic importance, is generally identified on the basis of benthic foraminiferal assemblages (Skinner, 1966).

Finally, in interpreting paleodepths by fossil populations of extant species, the depth preferences of modern foraminifera have to be used with an understanding of past water-masses. Recent paleoceanographic investigations indicate that depth adaptations of some bathyal foraminifera changed in middle or late Cenozoic times, because of changes in water-mass boundaries. For instance, the upper depth limit of Melonis pompilioides, now about 2300 m in the eastern Pacific, was about 1400 m during the last glaciation, because of the shoaling of the upper boundary of the Pacific Deep Water (Blake and Douglas; see Douglas, 1979). This finding invalidates a previous conclusion that the California borderland has been uplifted about 1000 m during the Holocene.

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