

S-11A-C Lambridg

# B R E V I O R A

MUS. COMP. ZOOL.  
LIBRARY

Museum of Comparative Zoology

APR 8 1974

US ISSN 0006-9698

CAMBRIDGE, MASS. 29 MARCH 1974

HARVARD  
NUMBER 420  
UNIVERSITY

## ENVIRONMENTAL FACTORS CONTROLLING THE DISTRIBUTION OF RECENT BENTHONIC FORAMINIFERA

GARY O. G. GREINER\*

### EDITORIAL INTRODUCTION

*Gary Greiner lost an eight-year battle with cancer and died in January 1973 at the age of 31. His unconventional approach to paleontology belied the painfully shy and unassuming character that many might have taken, so wrongly, as marks of merely ordinary ability. He was an original and radical thinker, limited, frustrated, even exasperated, by the reception that must attend unconventional ideas (be they right or wrong). And it was his special tragedy that illness, with its ultimate and ineluctable result, struck even before he began his research and robbed him of energy and time to test the ideas that flowed so readily.*

*Gary was captivated by D'Arcy Thompson's approach to form — to the reduction of organic complexity to a few, simple generating factors related to physical forces in the environment. D'Arcy Thompson overstated his case for the complex Metazoa, but it represents an insight scarcely explored (though surely more appropriate) for simpler Foraminifera. Gary asserted this theme within a traditional area of natural history fundamentally hostile to it (foraminiferal systematics) — an area that catalogues the specific, the unusual and the peculiar in preference to extracting the simpler regularities that have both general significance and frequent exceptions.*

*This paper represents Gary's views on the control of relative abundances by a simple environmental factor. Specialists will recognize some exceptions among forams in other parts of the*

\*Request reprints from Stephen Jay Gould, Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138.

world. They may disagree with his unsupported speculations on the significance and mode of formation for different types of calcareous walls. Yet the data on distribution are firm and must be explained. We hope that readers will focus on the power of Gary's unconventional approach, on his search for reduction and cause in preference to elaboration and minute, thoughtless description.

As an appendix, we attach the short text of a talk delivered to the annual meeting of the Geological Society of America in 1970. It supplements, in a broader evolutionary context, the central notion of physical control so central to the functional theme of causal correlation between environment and form. We report with the greatest regret that we were unable to reconstruct Gary's major work from his fragmentary notes and copious data—a bold attempt to synonymize virtually all the agglutinating Foraminifera of the Gulf of Mexico by showing that the entire range of form (now attributed to several genera) can be generated automatically by the interaction of a varying environment and the few parameters (*sensu* Raup and Vermeij) needed to specify construction of the seemingly complex foraminiferal test.

Gary wrote the following paper during a post-doctoral year at the Museum of Comparative Zoology. It was our privilege to have known, better than most others, such a courageous and talented person.

Stephen Jay Gould  
Alan D. Hecht

**ABSTRACT.** The relative abundance distributions of the three major groups of benthonic Foraminifera (agglutinated, porcelaneous, and hyaline calcareous) from the northern Gulf of Mexico paralic environments have been studied to determine the environmental factor, or factors, actually controlling the distribution. The relative contribution of each type to the total foraminiferal fauna is related to temperature and/or salinity within each bay studied, and to regional gradients in temperature and salinity (expressions of climatic and physiographic interactions) throughout the northern Gulf estuaries.

I conclude that these correlations can be explained on the basis of foraminiferal interaction with a single environmental factor—availability of calcium carbonate for use in construction of tests. This factor depends, to a large extent, on salinity and temperature in shallow, marine or brackish waters.

Agglutinated Foraminifera do not require calcite to build their test; they dominate the faunas in areas of low  $\text{CaCO}_3$  availability. Porcelaneous Fora-

minifera employ no nucleating surface for calcite crystal growth; crystals develop in a random array within a cytoplasmic layer. They dominate in areas of high  $\text{CaCO}_3$  availability, but diminish in abundance toward lower values owing to difficulties in secretion of calcite. Hyaline calcareous Foraminifera produce oriented calcite crystals grown on an organic nucleating surface. This surface permits secretion of calcite for test construction in areas of lower  $\text{CaCO}_3$  availability than is possible for the porcelaneous types, but the need for an ordered structure prevents their thriving in areas of hyper-supersaturation. Calcareous Foraminifera can dominate agglutinated types when  $\text{CaCO}_3$  is readily available, through occupation of niches unavailable to the latter (*e.g.*, on marine plants). Thus, hyaline calcareous Foraminifera dominate in areas of intermediate  $\text{CaCO}_3$  availability.

If we accept this simplistic approach to the study of Foraminifera, then its ramifications might have far-reaching effects in the study of foraminiferal paleoecology, since the applications would be independent of specific or generic classification.

## INTRODUCTION

Most ecologic studies of Recent Foraminifera have dealt with distributions of the various *species* or *genera* present in a particular area, and with the correlation of these distributions with various environmental parameters. The reasons for these correlations are difficult to ascertain; hence, the applicability to the fossil record of conclusions based on such correlations is often doubtful. To extend ecological inferences of a particular faunal group to paleontologic situations, an understanding of environmental interactions with morphologic characteristics transcending specific or generic classifications should be sought.

I chose foraminiferal wall type as the character to investigate (Greiner, 1969). In standard classifications (Loeblich and Tappan, 1964), wall type is used to separate the three major groups of Foraminifera into suborders — the Textulariina (agglutinated walls), the Miliolina (porcelaneous, calcitic walls), and the Rotaliina (perforate, hyaline calcareous walls). If the influence exerted by the environment on the distribution of these separate suborders could be recognized, the information gained could reasonably be extrapolated to paleoecologic interpretations of faunas as early as the beginning of the Mesozoic Era when calcareous Foraminifera were becoming abundant.

In the Recent, the relative contributions of each of these groups to the total fauna vary systematically across the continental shelf, from one bay to another, and from boreal waters to the tropics. That these changes are systematic and simple, rather than sporadic and complex, suggests that the abundances

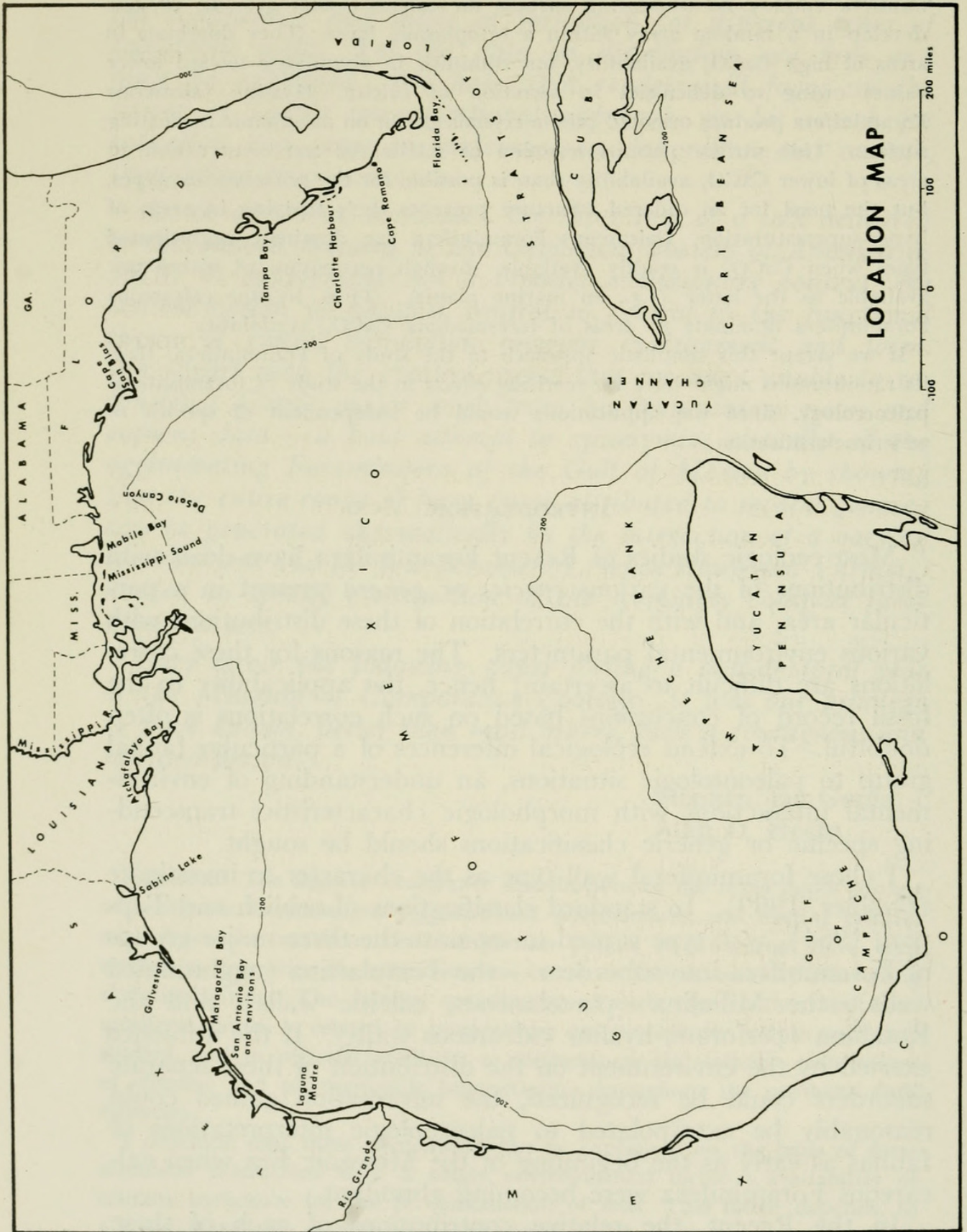


Figure 1. Location map.

of the foraminiferal suborders are being controlled by some general property of the environment, and that this property also varies simply and systematically. I assumed that a careful analysis of these distributions in relation to general environmental parameters would result in *correlations* leading to an understanding of the actual *controlling* factor or factors. Depth, the one factor suggested by Phleger (1960a) as most significant in controlling distributions of foraminiferal species in offshore traverses, can be essentially eliminated from consideration by investigation of faunas in very shallow water bodies — bays, lagoons, and sounds. Variation in the faunas can then be ascribed to some other environmental factor, such as temperature, salinity, character of the substrate, or some critical combination of several of these.

Foraminiferal faunas and general environmental parameters have been described for many of the larger bays, lagoons, and sounds adjacent to the northern Gulf of Mexico (Fig. 1). Since we have adequate literature on these shallow water bodies and since they form a geographic, as well as an environmental, continuum, they have been chosen for more complete analysis.

The purposes of this study are, then, to describe the relative abundance distributions of the three major groups of benthonic Foraminifera in the estuarine environments of the northern Gulf of Mexico; to relate these distributions to physical and chemical parameters of the environment; to review the more recent literature pertinent to the understanding of physiologic mechanisms employed by the foraminifers in constructing each wall type; and, finally, to summarize the environmental factors and relate them to the physiologic processes of wall construction by these protists, with a view to determining the actual *causes* of distribution at this morphologic level.

The results, it is hoped, will have a general significance for the interpretation of the paleoenvironments and paleoclimates of geologic epochs prior to those populated by species that still exist today.

#### PREVIOUS STUDIES OF FORAMINIFERAL ECOLOGY

The early works on Recent foraminiferal ecology (*e.g.*, Parker, 1948; Phleger and Parker, 1951; Parker, Phleger, and Peirson, 1953; and Bandy, 1956) were largely taxonomic, with descriptions of species distribution in relation to depth and geographic position, based on relative abundances at each sample locality.

Various environmental parameters were invoked to explain the apparent natural breaks in faunal patterns. Since depth and proximity to the shore and continental shelf break had been measured, and since little else was known about the environment of the open ocean, discontinuities in the distributions were correlated with these factors.

Later studies show similar approaches to the problem of causes for the observed distribution patterns. A notable example is that of Lidz (1965), who observed intercorrelations of various environmental factors and species distributions measured in Nantucket Bay, Massachusetts. The most that could be said, based on the correlations, is that all of the factors are interrelated and correlated with one another, *i.e.*, the environmental factors are, to varying degrees, dependent variables. But nothing can be said about actual *causes* of the foraminiferal distributions.

Phleger (1960a), in discussing the ecology and distribution of Recent Foraminifera, states that the *causes* of depth zonation and other distribution patterns are not clearly known. The factors involved (he states) are temperature, salinity, food, water chemistry, pressure, currents, turbidity, turbulence, substrate, biologic competition, disease, etc. And in summarizing this long list, he states that at the present state of our knowledge it is not possible to evaluate any one of these factors. In a later report of the state of the field (Phleger, 1964), he indicates that ". . . there is little or no specific information on the interactions between the patterns of benthonic foraminiferal faunas and the natural environments which control these patterns."

A few, more current papers reflect this state of affairs and illustrate attempts to define characteristics of foraminiferal populations (diversity, planktonic/benthonic ratios, general morphology, etc.) which transcend specific or generic characteristics and which are explicable in terms of the environment (Bandy and Arnal, 1960; Bandy, 1964; Phleger, 1964; Stehli, 1966; Wantland, 1967).

Funnell (1967) summarizes our knowledge of foraminiferal ecology in a discussion of Foraminifera as depth indicators in the marine environment. He suggests that since Foraminifera are studied with relation to depth, and depth has so many factors correlated to it, we can construct good interpretations for the Tertiary of, say, the Gulf Coast as compared to the Recent Gulf of Mexico, but that these same conclusions will not be necessarily valid for the Tertiary of, for example, northwestern Europe, or for the pre-Tertiary of the Gulf Coast.

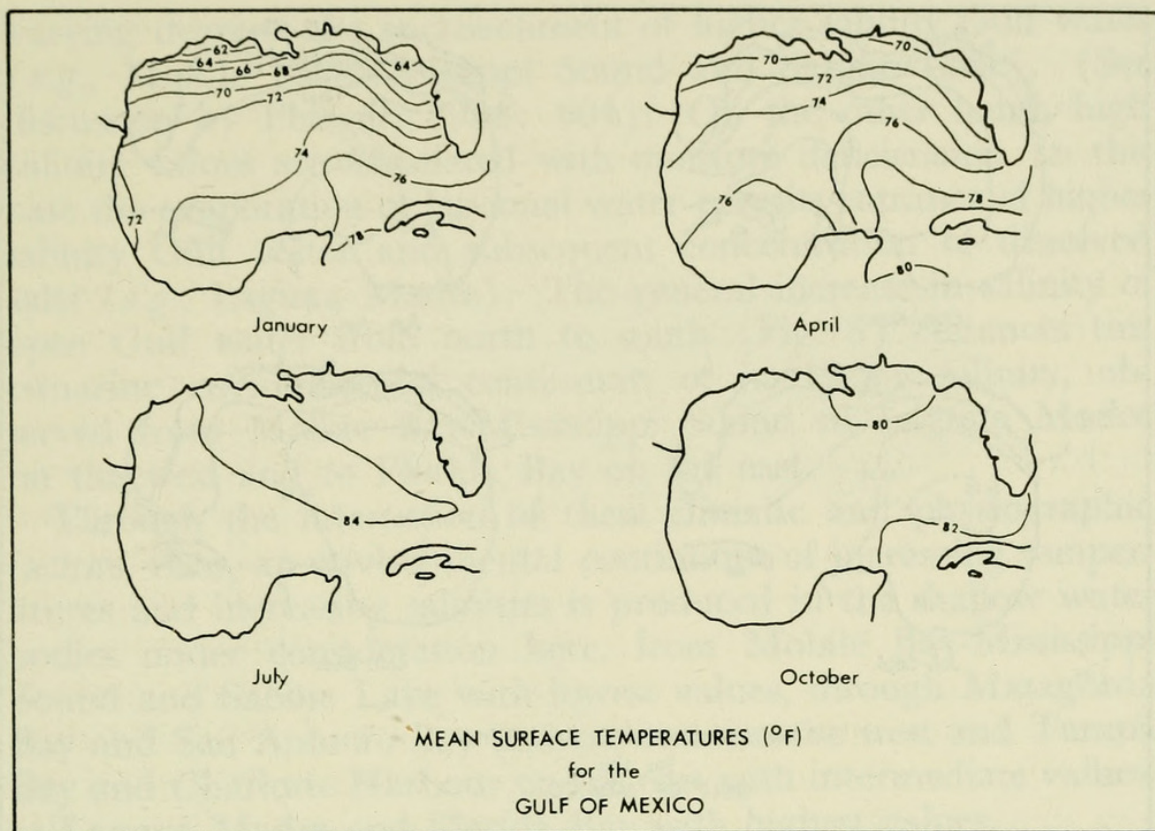


Figure 2. Mean surface water temperatures during four months of the year for the Gulf of Mexico. (Redrawn from charts supplied by the National Oceanographic Data Center, 1966.)

Clearly then, the *causes* of various trends in foraminiferal faunas must be established, if situations in the fossil record fundamentally dissimilar to the time or area of Recent investigations are to be treated profitably.

#### PHYSICO-CHEMICAL SETTING OF THE GULF OF MEXICO

The coastal United States bordering the northern Gulf of Mexico is generally a broad, low-lying plain. The near-shore, shallow-water environments are made more complex by the presence of many barrier islands closely paralleling the coastline and often restricting the free interchange of river and open Gulf waters. The presence of the barrier islands produces many bays, lagoons, and sounds (Fig. 1), which harbor faunas distinct from those of the open Gulf. The temperatures and salinities of the water in these estuarine environments are a result of the interaction of various climatic and physiographic parameters of the region.

There is a definite increase in mean annual temperature (re-

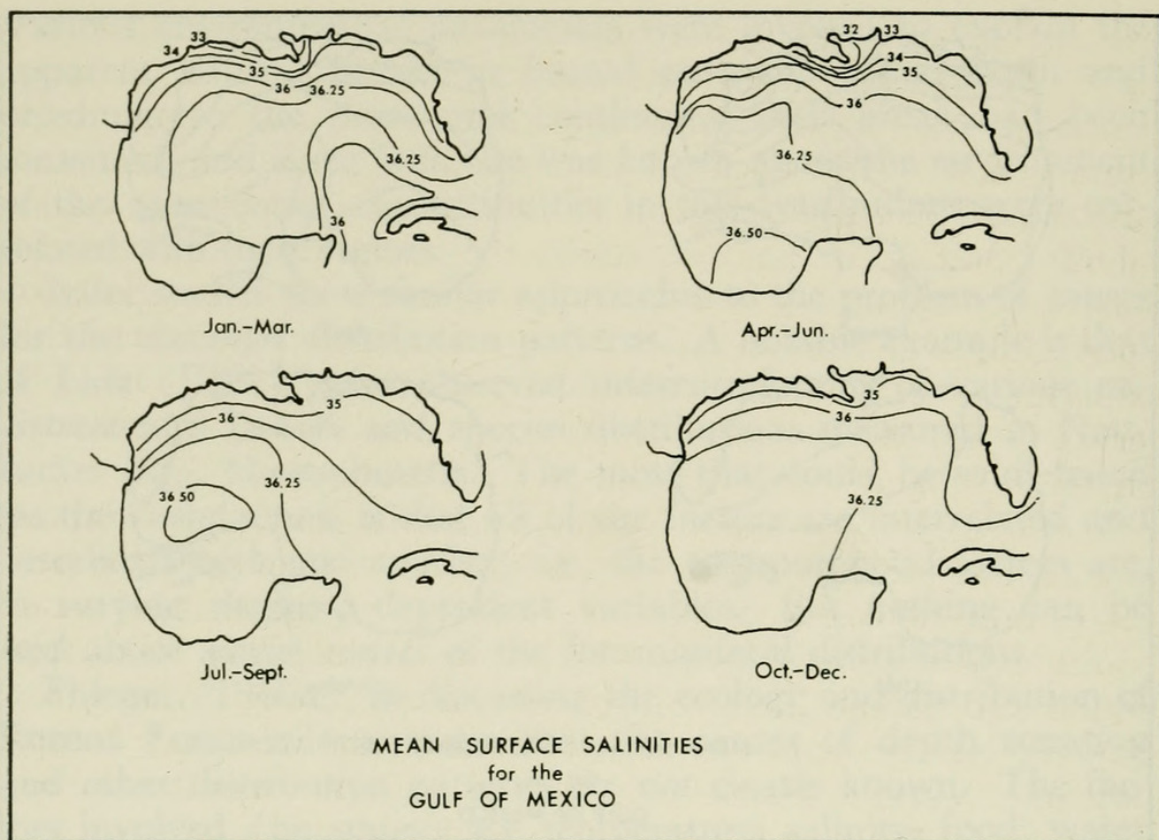


Figure 3. Mean surface water salinity during four seasons of the year for the Gulf of Mexico. (Redrawn from charts supplied by the National Oceanographic Data Center, 1966.)

flected in the Gulf surface water temperatures, Fig. 2; and in the January normal isotherms of Fig. 9) from north to south across the region. Since the bays are generally quite shallow, and hence the water well-mixed by wind, temperatures in them tend to correspond to air temperatures. Thus, mean annual water temperatures in the estuarine environments around the northern Gulf are lowest in Mobile Bay-Mississippi Sound and Sabine Lake, and increase in the more southern bays, being highest in Florida Bay and Laguna Madre.

Salinity values in the bays similarly show an increase from north to south. This is the result of several interrelated factors—precipitation, runoff, evaporation, and salinity of adjacent Gulf water (Fig. 3). The first three factors have been studied by Thornthwaite (1948) and the net effect plotted on a map as moisture budget isopleths (reproduced here as part of Fig. 9), which are an indication of moisture surplus (positive values) and moisture deficit (negative values). In general, low salinity values in the bays are associated with high moisture surpluses, as fresh-water influx into an enclosed shallow water body prevents, to

varying degrees, the encroachment of higher salinity Gulf water (*e.g.*, Mobile Bay-Mississippi Sound and Sabine Lake). (See discussion by Phleger, 1954: 604). On the other hand, high salinity values are associated with moisture deficiencies. In this case the evaporation of lagoonal water permits entrance of higher salinity Gulf water and subsequent concentration of dissolved salts (*e.g.*, Laguna Madre). The general increase in salinity of open Gulf water from north to south (Fig. 3) enhances this estuarine environmental continuum of increasing salinity, observed from Mobile Bay-Mississippi Sound to Laguna Madre on the west and to Florida Bay on the east.

Through the interaction of these climatic and physiographic factors, then, an environmental continuum of increasing temperatures and increasing salinities is produced in the shallow water bodies under consideration here, from Mobile Bay-Mississippi Sound and Sabine Lake with lowest values, through Matagorda Bay and San Antonio Bay and environs on the west and Tampa Bay and Charlotte Harbour on the east with intermediate values, to Laguna Madre and Florida Bay with highest values.

#### DISCUSSION OF FORAMINIFERAL DISTRIBUTIONS

From published tables of species abundances in various estuarine environments around the northern Gulf of Mexico, I calculated the relative abundance of individuals possessing each of the three major wall types at given sample locations. This is based on percentage of individuals in the total (living plus dead) foraminiferal fauna. I then plotted these percentages on maps of the sample distributions and contoured the values.

The relative abundance distribution of the three foraminiferal groups will be discussed in detail for three of the estuarine environments — Mobile Bay-Mississippi Sound, Tampa Bay, and Laguna Madre — and more broadly for the others, to demonstrate correlations with temperature and salinity on the local scale. Following this, I will consider the faunal dominance by each of the groups through all the bays, lagoons, and sounds adjacent to the northern Gulf to document similar correlations with these environmental factors on a regional scale.

##### MOBILE BAY-MISSISSIPPI SOUND

The distribution of Foraminifera and possible ecologic factors affecting the distribution in Mobile Bay, Alabama, have been briefly mentioned by Walton (1964). Phleger (1954) has made

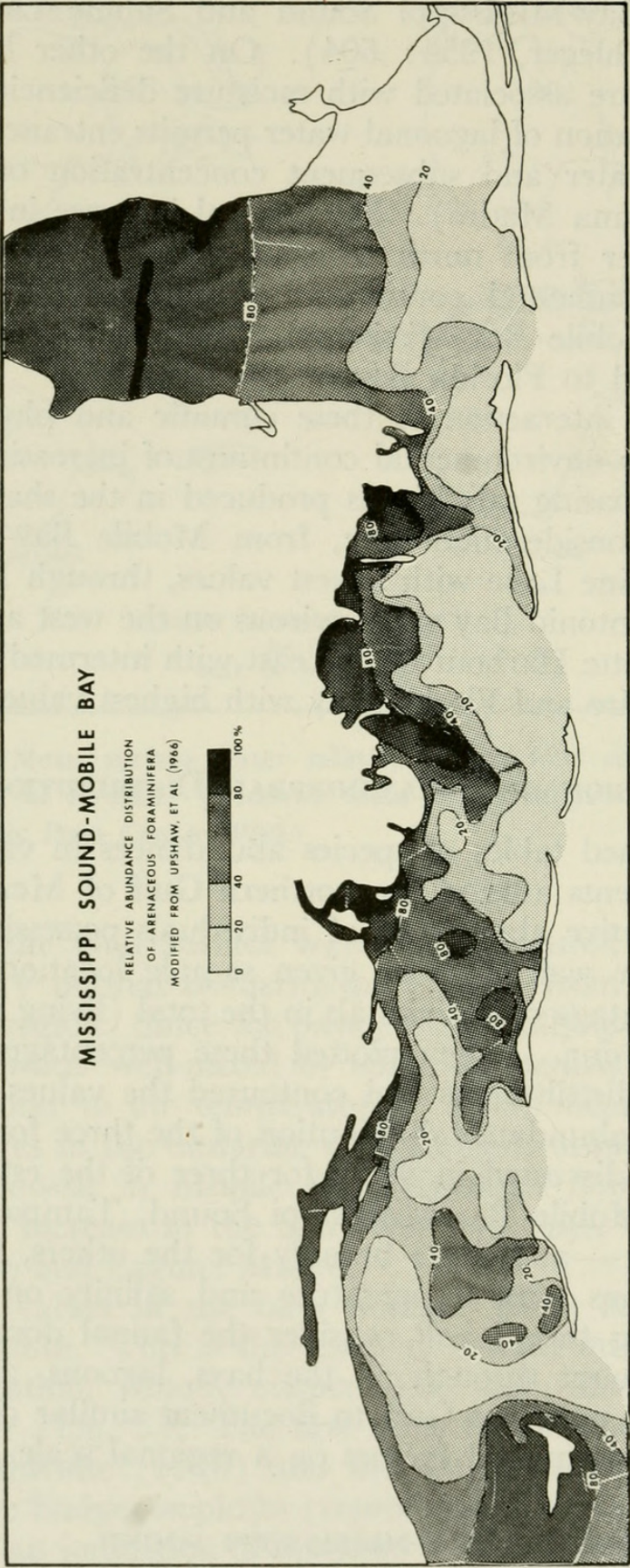


Figure 4. Relative abundance distribution of agglutinated Foraminifera from Mobile Bay-Mississippi Sound. (After Upshaw *et al.*, 1966.)

a similar but more detailed study of the Mississippi Sound. Upshaw *et al.* (1966) have studied and described the environment, sediments, and microfauna from both areas plus a portion of the adjacent continental shelf (Fig. 4).

There is a considerable moisture excess for this region (Thornthwaite, 1948; and Fig. 9). This results from many large rivers discharging fresh water into Mobile Bay (Mobile and Tensaw rivers) and Mississippi Sound (particularly the Pascagoula River). The offshore, discontinuous island chain is an effective barrier to ready mixing of this runoff with the open Gulf water (Phleger, 1954). However, some denser, more saline water from the Gulf does enter Mississippi Sound by way of the surge channels and mixes with the fresh water from the rivers within this shallow water body. Thus, there is a steep salinity gradient in bottom waters from the open Gulf (with usually  $35^{\circ}/\text{oo}$ ), through the adjacent inlet (near  $30^{\circ}/\text{oo}$ ), and into Mobile Bay-Mississippi Sound (to  $< 5^{\circ}/\text{oo}$  within 10 miles of the Gulf).

From the foraminiferal distribution data of Upshaw *et al.* (1966, plate 4, reproduced here as Fig. 4), it is evident that the agglutinated Foraminifera are relatively most abundant in water with the lowest salinity values, and that they decrease in relative abundance with increasing salinity. On the other hand, the hyaline calcareous Foraminifera are associated with the more saline Gulf water, diminishing in relative abundance as it is diluted by fresh water within the bay and sound. Representatives of the third group, the porcelaneous Foraminifera, are not found within this restricted area, though they are present (up to 30% or more) in the more saline Gulf water somewhat seaward of the freshwater influence. Hence, the relative abundance distributions of two of the foraminiferal groups are correlated here with water salinity values — hyaline calcareous directly, agglutinated inversely.

#### TAMPA BAY

Bandy (1956) and Walton (1964) have made ecologic studies of the Foraminifera of Tampa Bay and environs, including Old Tampa Bay (Walton, 1964) and Hillsboro Bay (Bandy, 1956).

Bathymetrically, the bay can be divided into low sand and grass flats of shallow depth ( $< 15$  ft. of water) with superimposed relatively deep channels (Goodell and Gorsline, 1960). Maximum depth in the bay is slightly more than 30 feet, which



is that of most of the channels (Fig. 5). The sediments of Tampa Bay are predominantly fine to very fine quartz sands (Walton, 1964).

The salinity distribution pattern for Tampa Bay and environs can be qualitatively described as follows: In the channels dissecting the bottom topography, the water salinity is at a maximum near the mouth of the bay complex (somewhat above 'normal' marine), with a very slight gradient to lower salinities in Hillsboro Bay. The adjacent shoal waters have a similar gradient, from near normal marine salinity at the mouth of Tampa Bay to lowest salinities (just slightly above that of river water) in upper Hillsboro Bay. Since the salinity in the channels is everywhere higher than that of the adjacent sand and grass flats, there is also a positive gradient from shallow to deep water.

The relative abundance distributions of the agglutinated and the porcelaneous Foraminifera are shown in Figures 6 and 7, respectively. The changing contributions of these two groups and that of the hyaline calcareous group reflect the salinity gradients just discussed.

These foraminiferal distributions clearly demonstrate a strong correlation between salinity and the relative abundances of each of the three groups. Highest salinity waters characteristically have high percentages of the porcelaneous type associated with them. In successively lower salinities, the hyaline calcareous type and then the agglutinated type reach their maximum relative abundances.

#### LAGUNA MADRE

Laguna Madre is located within the semi-arid climatic zone of Thornthwaite (1948), and, hence, has a more or less persistent, marked moisture deficiency (Fig. 9). There are no major rivers flowing into the area, and there is only very slight fresh-water inflow from ephemeral streams during local rainfall (Rusnak, 1960). The excess of evaporation over precipitation allows the normal marine Gulf waters to enter the shallow basins (average depth, about  $2\frac{1}{2}$  ft.) of Laguna Madre and causes the water there to be generally hypersaline. Chlorinities in the northern basin range from 22 to 45‰ Cl and in Baffin Bay from 1 to 45‰ Cl; the southern basin, with lower salinities, has up to 35‰ Cl (Phleger, 1960b).

The temperature of the lagoonal water reflects that of the air (Phleger, 1960b); and because of the positive thermal gradient

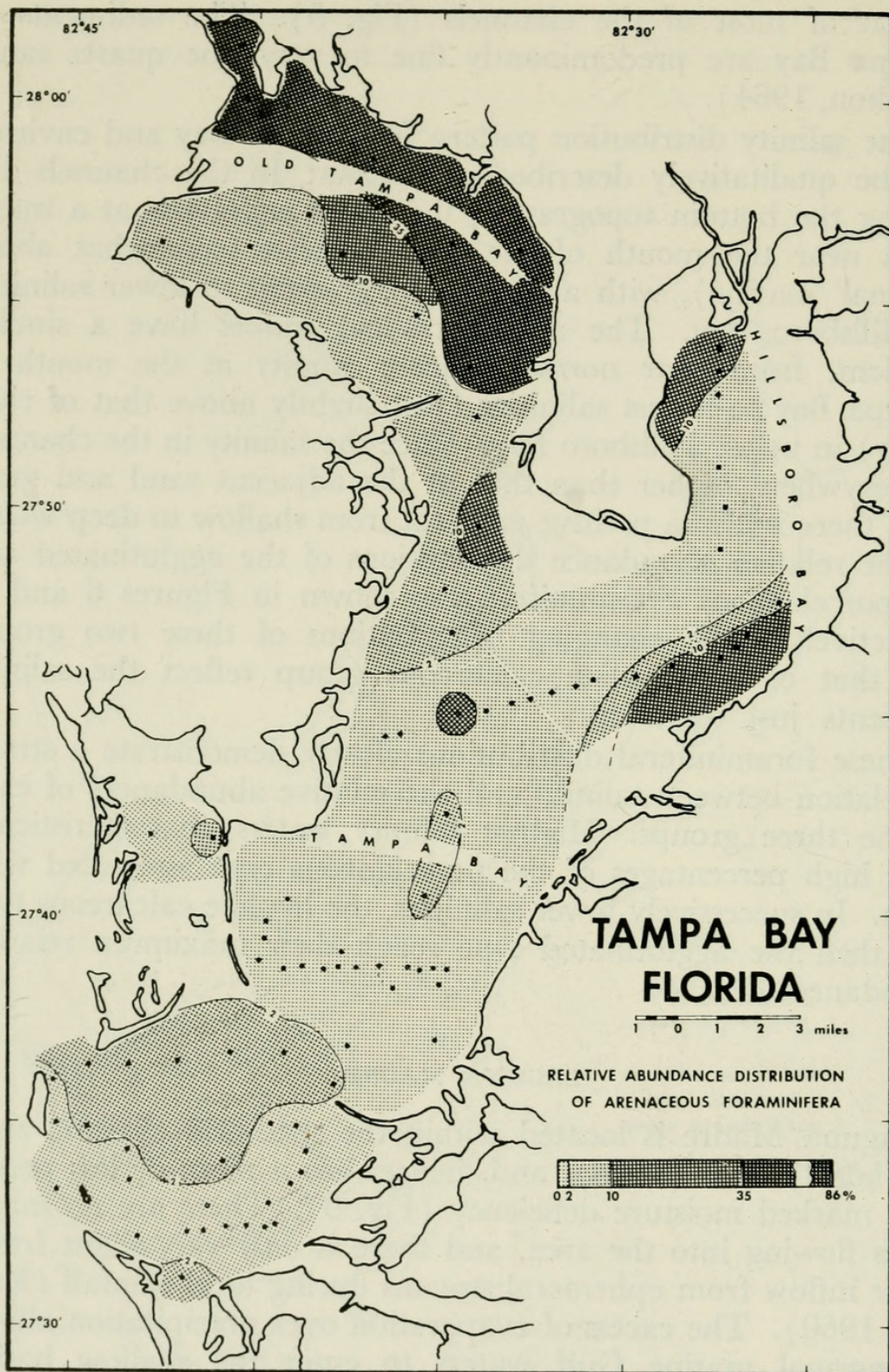


Figure 6. Relative abundance distribution of agglutinated Foraminifera from Tampa Bay, Florida. (Data from Bandy, 1956; and Walton, 1964.)

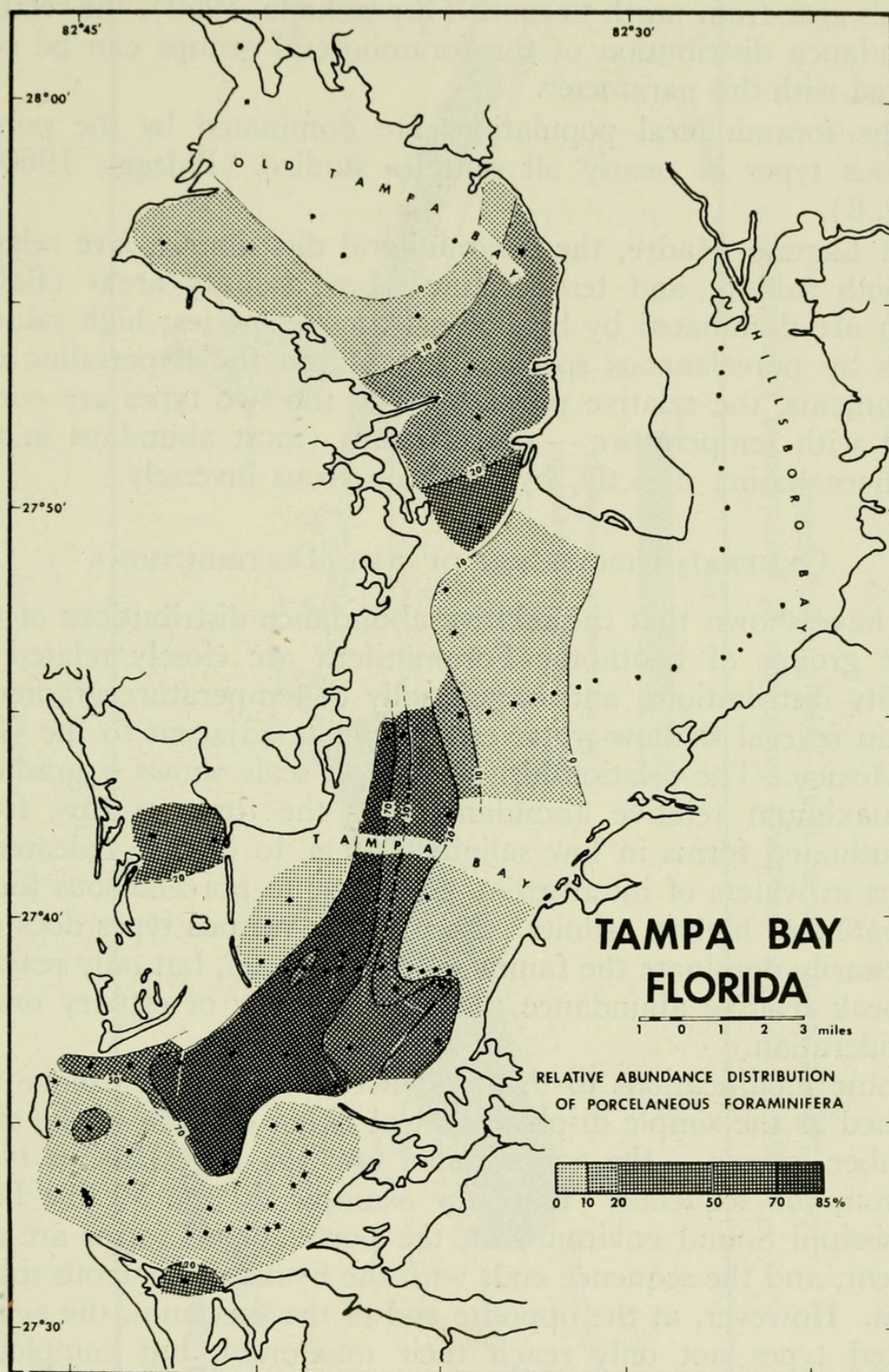


Figure 7. Relative abundance distribution of porcelaneous Foraminifera from Tampa Bay, Florida. (Data from Bandy, 1956; and Walton, 1964.)

in this area from north to south (Espenshade, 1960), the relative abundance distribution of the foraminiferal groups can be correlated with this parameter.

The foraminiferal populations are dominated by the porcelaneous types in nearly all samples studied (Phleger, 1960b) (Fig. 8).

In Laguna Madre, the foraminiferal distributions are related to both salinity and temperature. Low salinity areas (Baffin Bay) are dominated by hyaline calcareous species; high salinity areas by porcelaneous species. But within the hypersaline environments, the relative proportions of the two types are correlated with temperature — porcelaneous (most abundant in the southern basin) directly, hyaline calcareous inversely.

#### GENERAL DISCUSSION OF THE DISTRIBUTIONS

I have shown that the relative abundance distributions of the three groups of benthonic Foraminifera are closely related to salinity distributions, and occasionally to temperature gradients, within several shallow-water environments adjacent to the Gulf of Mexico. The relationship on a *local* scale shows a gradient of maximum relative abundances for the three groups, from agglutinated forms in low salinity waters, to hyaline calcareous forms in waters of intermediate salinities, to porcelaneous forms in waters of highest salinity. Each of the various types does not necessarily dominate the fauna at its maximum, but only reaches its peak relative abundance there for the bay or estuary under consideration.

Some modifications to this sequence occur. Most can be explained as the simple displacement of either or both of the end-member groups — the agglutinated and the porcelaneous types — from the sequence. Thus, for example, in the Mobile Bay-Mississippi Sound environment, the porcelaneous forms are not present, and the sequence ends with the hyaline calcareous maximum. However, at the opposite end of the spectrum, the agglutinated types not only reach their maximum, but completely dominate the upper bay fauna to the exclusion of any calcareous forms. This situation is correlated with a much higher runoff and consequent lower salinity for this estuary than for most of the others.

On the other hand, the samples from Laguna Madre yielded almost no agglutinated Foraminifera while the hyaline calcareous forms reach their maximum abundance in waters of the lowest

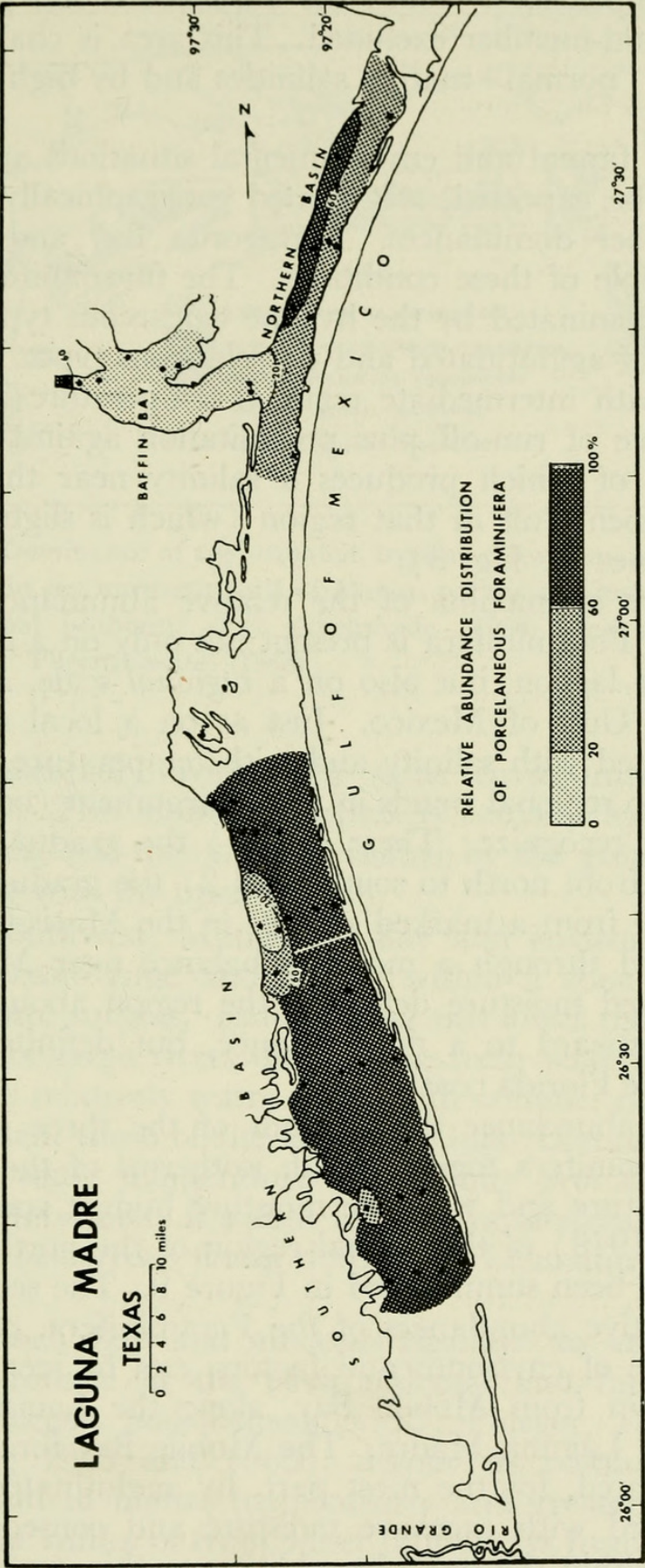


Figure 8. Relative abundance distribution of porcelaneous Foraminifera from Laguna Madre, Texas. (Data from Phleger, 1960b.)

salinity and temperature. Thus, the sequence is still preserved, but with one end-member excluded. This area is characterized by higher than "normal" marine salinities and by high temperatures.

Intermediate faunal and environmental situations are present and, as might be expected, are located geographically between these end-member dominances. Matagorda Bay and environs is a good example of these conditions. The foraminiferal fauna is everywhere dominated by the hyaline calcareous types, to the near exclusion of agglutinated and porcelaneous types. This can be correlated with intermediate regional temperatures and with the close balance of run-off plus precipitation against evaporation, the latter of which produces a salinity near the normal value for the open Gulf in that region (which is slightly below "normal" marine; cf. Fig. 3).

This sequence in maxima of the relative abundances of the three groups of Foraminifera is present not only on a *local* scale within a bay or lagoon, but also on a *regional* scale, across the entire northern Gulf of Mexico. Just as on a local scale, the trend is correlated with salinity and with temperature.

There are two regional trends in the environment (or climate) which we must recognize. These are: 1) the gradual increase in *temperature* from north to south; and 2) the gradual shift in *moisture budget* from a marked surplus in the Mississippi Delta region, westward through a moisture balance near Matagorda Bay, to a marked moisture deficit in the region about Laguna Madre, and eastward to a near balance, but definite surplus, along most of the Florida coast.

The relative abundance distributions of the three groups of benthonic Foraminifera together with isotherms of the January normal temperature and with the moisture budget zones (after Thornthwaite, 1948) of the coastal region of the northern Gulf of Mexico have been summarized in Figure 9. The sequence in maxima of relative abundances of the Foraminifera, correlative with a sequence of environmental factors, can be seen as a regional continuum from Mobile Bay, along the Louisiana and Texas coasts, to Laguna Madre. The Mobile Bay foraminiferal fauna is dominated, for the most part, by agglutinated species. This is correlated with excessive moisture and consequent low salinity water within the bay. In addition to this, mean annual temperatures are here near the lowest for the Gulf area.

Sabine Lake, the next area of study to the west, again has a fauna dominated by agglutinated species (Kane, 1967) and is

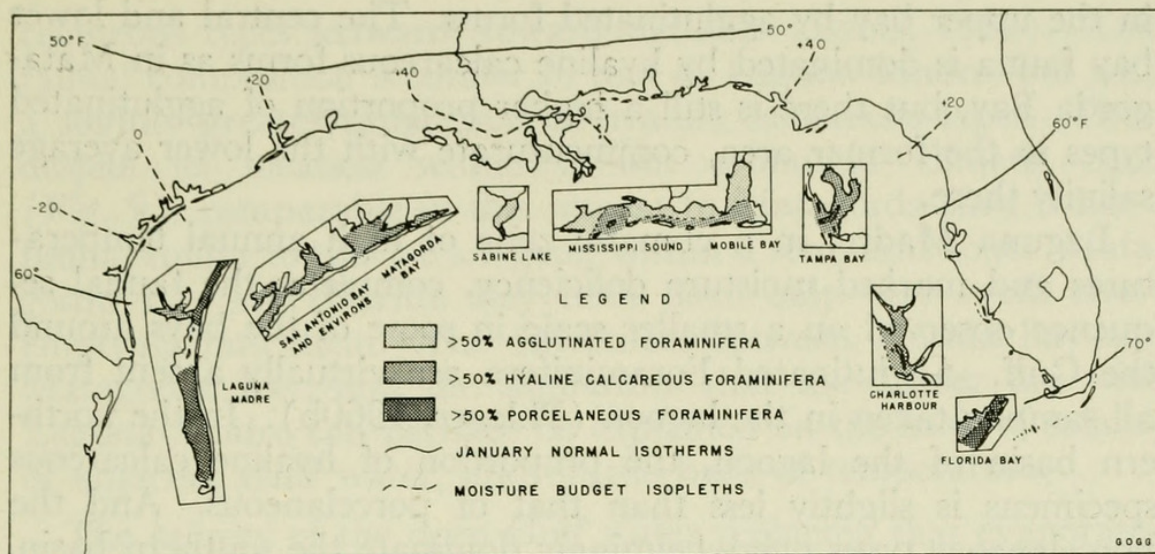


Figure 9. Dominance of agglutinated, hyaline calcareous, and porcelaneous Foraminifera in the northern Gulf of Mexico paralic environments; including January normal isotherms after Espenshade (1960), and moisture budget isopleths after Thornthwaite (1948).

included, essentially, within the same environmental zones as Mobile Bay. The moisture surplus is actually less than in the previous area, but this is compensated by the greater restriction from mixing with the open Gulf.

To the southwest, Matagorda Bay and environs is within a warmer climatic zone and is also within a zone of only very slight moisture surplus. Emphasizing this lower moisture surplus is the lack of large rivers discharging fresh water into the bay. The result is relatively warm water with salinities near, but somewhat less than, those of the adjacent Gulf. Commensurate with this rise in water temperature and salinity over that of Sabine Lake and Mobile Bay is a shift in the foraminiferal fauna. Here the hyaline calcareous forms dominate (Lehmann, 1957; Shenton, 1957).

San Antonio Bay and environs displays an anomalous, but explicable, reverse in the environmental and faunal sequence (Parker, Phleger, and Peirson, 1953; Phleger, 1956; Shepard and Moore, 1955 and 1960), despite its position within the climatic trend to higher temperatures and greater moisture deficiency. The influx of fresh water to the bays from the relatively large San Antonio-Guadalupe River system is the cause of the much lower water salinity values here than in Matagorda Bay, which is in a general area of greater moisture surplus. There is a correlative shift in the foraminiferal fauna to one dominated

in the upper bay by agglutinated forms. The central and lower bay fauna is dominated by hyaline calcareous forms as in Matagorda Bay, but there is still a higher proportion of agglutinated types in the former area, commensurate with the lower average salinity there.

Laguna Madre, in a climatic zone of high annual temperatures and marked moisture deficiency, completes the faunal sequence observed on a smaller scale in some of the bays around the Gulf. Agglutinated Foraminifera are virtually absent from all samples taken in the lagoon (Phleger, 1960b). In the northern basin of the lagoon, the proportion of hyaline calcareous specimens is slightly less than that of porcelaneous. And the porcelaneous types overwhelmingly dominate the southern basin. Hence, there is a direct correlation between temperature and the proportion of porcelaneous forms in the bottom sediment.

An environmental continuum and faunal dominance sequence similar to that just described can be documented for the Florida Gulf coast and correlated with climatic trends from Mobile Bay to Florida Bay. The change in moisture budget is not so dramatic as to the west, as a surplus is maintained along the entire coast to the tip of Florida (Fig. 9). However, the temperature gradient is even steeper, making Florida Bay approximately 6°C warmer than Laguna Madre during January, though both are at comparable latitudes.

The sequence in maxima of relative abundances of the three benthonic groups is developed and can be correlated with the general environmental trend to higher salinities and higher temperatures to the south. After Mobile Bay, with its overwhelming dominance of agglutinated Foraminifera, the next area to the south is Tampa Bay. The whole foraminiferal sequence is developed here, but the hyaline calcareous types dominate the fauna over the greater part of the bay, except in the deep channels. Charlotte Harbour and vicinity has a similar fauna, largely dominated by hyaline calcareous forms (data after Bandy, 1954), though the whole sequence is again present. Both of these areas are similar environmentally and climatically. Both are in the wet subhumid zone and both receive limited drainage from the surrounding, low-lying, karst topography. There is some difference in latitude and hence, in mean annual temperature, but this is minimal. Thus, the two areas have very similar foraminiferal faunas.

The fauna of Florida Bay is dominated in the near-shore, lower salinity areas by hyaline calcareous types, and by por-

celaneous types seaward, toward the keys (Lynts, 1962). This faunal composition is similar to that of Laguna Madre, but with a slightly greater proportion of hyaline calcareous types. Thus, despite its location within a wet subhumid climatic zone (Fig. 9), comparable in this respect to Matagorda Bay, it has a fauna similar to that of a lagoon within a semi-arid zone. Matagorda Bay and Florida Bay both have only very small rivers emptying into them. The differences between Florida Bay and Matagorda Bay, and the similarities that the former has with Laguna Madre can perhaps be explained on the basis of salinity of adjacent Gulf water, and on the basis of temperature.

The salinity of the open Gulf water replacing that evaporated from Florida Bay is somewhat higher than that entering Laguna Madre, and considerably higher than that available to Matagorda Bay (Fig. 2). Mean annual temperature at Florida Bay is somewhat higher than at Laguna Madre and considerably higher than at Matagorda Bay (Fig. 9). Thus, though the water of Florida Bay is diluted by runoff and precipitation similar to that for Matagorda Bay, it can be more quickly reconstituted to a higher salinity owing to greater evaporation and easier mixing with waters more saline than "normal" marine. It is also possible that the high proportion of porcelaneous Foraminifera should be correlated with the higher temperatures there, as I postulated for Laguna Madre.

To summarize the distributions and correlations discussed in this section, the following conclusions can be drawn. On a *local scale*, i.e., within a bay, lagoon, or other shallow-water environment, there is a succession of relative abundance maxima from agglutinated, through hyaline calcareous, to porcelaneous types; this is correlated with a trend in salinity or temperature values from low to high for the area. Also, either or both of the end-member types can be displaced from the sequence with commensurate shifts in the salinity and temperature gradients. These gradients are the most obvious factors of the environment to which the faunal sequence can be related. There are essentially uniformly shallow depths over most of the areas, and no apparent correlation of the faunal groups with bathymetry. Where several different sediment types are present within a single bay area, they are generally correlated with depth and, hence, not correlated with the fauna. In some areas, such as Florida Bay and Laguna Madre, a relative abundance sequence in the foraminiferal types is correlated with the temperature or salinity

gradient in each bay despite the uniformity of bottom sediment type.

*Regionally*, the same foraminiferal sequence is present — manifested in the various types dominating the population from bay to bay in succession. This sequence is again correlated with a general trend in salinity and temperature. This trend in the shallow-water environmental continuum is explicable in terms of climate and physiography of the adjacent coastal plain. The main climatic factors necessary for explanation are moisture balance and temperature. The influence of physiography on the local environment is evident in the amount of runoff carried into the various areas of investigation.

#### ENVIRONMENTAL FACTORS CONTROLLING DISTRIBUTION OF FORAMINIFERA

I present the hypothesis that the actual environmental factor controlling the distribution of Foraminifera is the *availability of calcium carbonate* (dependent, to a great extent, on salinity, temperature, and depth of water); or the ease with which these one-celled organisms can extract and precipitate  $\text{CaCO}_3$  for their test from the surrounding water.

*Chemistry.* Revelle (1934), in discussing the physico-chemical factors affecting the solubility of calcium carbonate in seawater, stated that, from the mass law equation  $\text{Ca}^{++} \times \text{CO}_3^{--} = {}^K\text{CaCO}_3$ , three parameters control the solubility of  $\text{CaCO}_3$ : concentrations of calcium and carbonate ions and the value of the temperature-dependent constant  ${}^K\text{CaCO}_3$ . "These factors are in turn dependent on salinity, temperature, hydrostatic pressure due to depth below the surface, carbon dioxide content, and the concentration of hydrogen and hydroxyl ions, as indicated by the  $\text{pH}$ " (Revelle, 1934: 103–104). Revelle and Fairbridge (1957: 256) conclude that the two most important processes facilitating the precipitation of calcium carbonate probably are: (1) an increase in temperature, which lowers the solubility of  $\text{CO}_2$ , thus increasing the carbonate ion concentration; and 2) evaporation, which increases the calcium ion concentration and carbonate alkalinity.

These two processes, governing the carbonate ion and calcium ion concentrations, respectively, can be equated with increasing temperature and increasing salinity. Thus, in low salinity and low temperature environments calcium carbonate will not be easily precipitated, owing to low calcium and low carbonate ion

concentration, the latter being largely a result of increased solubility of  $\text{CO}_2$  in the water. On the other hand, waters with high salinities and high temperatures, with their relatively high calcium and carbonate ion concentrations, are saturated or supersaturated with respect to calcium carbonate, as in tropical and subtropical surface seawater (Chave and Schmalz, 1966). In these areas calcium carbonate will be precipitated most readily.

Thus, all of the environmental parameters tend to increase the availability of calcium carbonate from the Mississippi Delta region toward the Rio Grande on the west, and toward Florida Bay on the east. This trend is closely correlated with the observed trend in relative abundance distributions of the foraminiferal groups studied (see Fig. 9 for a summary of climatic factors and the foraminiferal distributions).

From these observations, it is apparent that agglutinated Foraminifera are relatively most abundant in areas with the lowest availability of calcium carbonate. Porcelaneous Foraminifera, on the other hand, are associated with high availability of calcium carbonate, and often dominate the foraminiferal faunas of warm, saline tropical or subtropical waters. Finally, the areas characterized by intermediate calcium carbonate availability are dominated by the hyaline calcareous Foraminifera. This generalization is true on nearly all scales of observation: within a bay or lagoon, among several adjacent bays of a region, on contiguous portions of the continental shelf (Greiner, 1970), and on a worldwide scale.

*Mechanism.* The agglutinated Foraminifera do not require the precipitation of calcium carbonate in construction of their tests. They utilize the available sediment grains, cementing them together with a predominantly organic material (Hedley, 1963; Towe, 1967). They are therefore free of restriction to any of the marine or estuarine environments. The calcareous Foraminifera (both hyaline calcareous and porcelaneous), on the other hand, require calcium carbonate for the construction of their tests. The extent to which its availability is required depends upon the ability of the organism to concentrate and secrete (or allow precipitation of) calcium carbonate against (or within) the chemical environment of the water. I suggest that a fundamental distinction between the hyaline calcareous and the porcelaneous Foraminifera lies herein.

Electron microscope studies (Hay, Towe, and Wright, 1963; Towe and Cifelli, 1967; Lynts and Pfister, 1967) have shown that there is a radical difference between the shell structure of

porcelaneous Foraminifera and that of the hyaline calcareous types. In the porcelaneous wall there is a thick, inner layer with a three-dimensionally "random" array of elongate crystals and a pavement-like, surface veneer that in part exhibits preferred orientation. The hyaline calcareous wall, on the other hand, is made up of calcite crystals with a preferred orientation, the whole wall being penetrated by numerous pores, which are visible under the light microscope as well (Towe and Cifelli, 1967). These observations are consistent with the general separation (Loeblich and Tappan, 1964) of the hyaline calcareous and the porcelaneous wall types on the basis of perforations of one type and porcelaneous appearance of the other.

Lynts and Pfister (1967) have pointed out the differences in crystallization of the wall as observed for these two test types. One species with a hyaline calcareous wall was observed in the process of chamber formation (Angell, 1967a and b). The foraminifer, when beginning to add a new chamber, extended a portion of its protoplasm through the aperture of the test, forming a bulbous drop with the exact shape of the prospective chamber. An organic sheath formed on the surface of the drop. Shortly thereafter, protoplasm was again exuded (through the new aperture in the organic sheath) and covered, in a thin film, the surface of the new, tectinous chamber wall. Calcite crystals were then observed to nucleate on the organic surface and to grow upward (perpendicular to the surface) within the exuded cytoplasm, until the calcareous wall was complete. Observations by Towe and Cifelli (1967) suggest that other hyaline calcareous species also nucleate calcite crystals for test formations on an organic base.\*

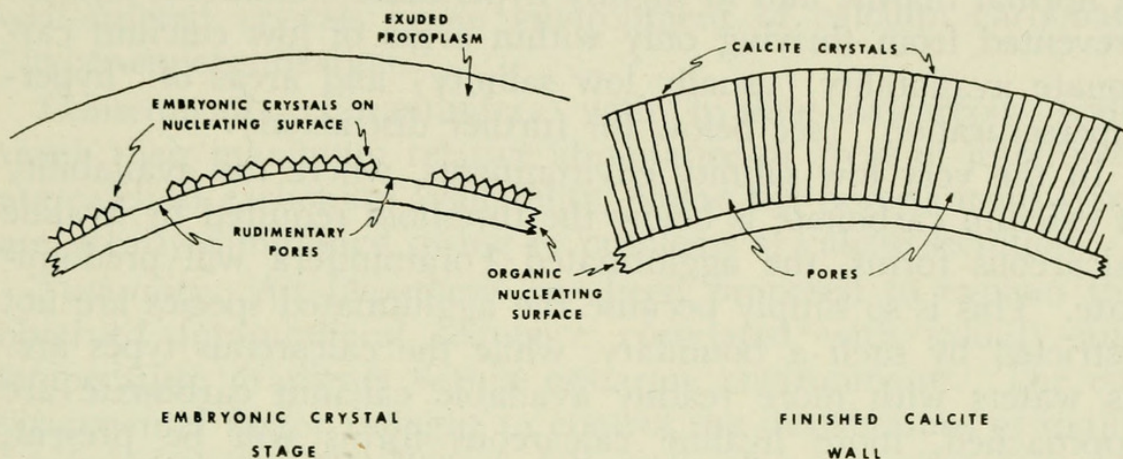
Arnold (1964), while observing chamber formation of a porcelaneous species (similar to that of hyaline calcareous types up to the secretion of calcite), noted that the calcite crystals grew in "random" fashion within the organic matrix formed by the exuded cytoplasm of the protist, not upon an organic nucleating surface (see Fig. 10 for a diagrammatic comparison of crystal growth in the two types). Lynts and Pfister (1967) have pointed out this difference between these two test types, and Towe and Cifelli (1967), likewise, conclude that porcelaneous wall structure is significantly different from hyaline calcareous.

I suggest that the absence of a nucleating surface for the se-

---

\*Subsequent work by Towe (1972) suggests that this may not be true for all Foraminifera in this group.

### SCHEMATIC DEVELOPMENT OF HYALINE CALCAREOUS WALL TYPE



### SCHEMATIC DEVELOPMENT OF PORCELANEUS WALL TYPE

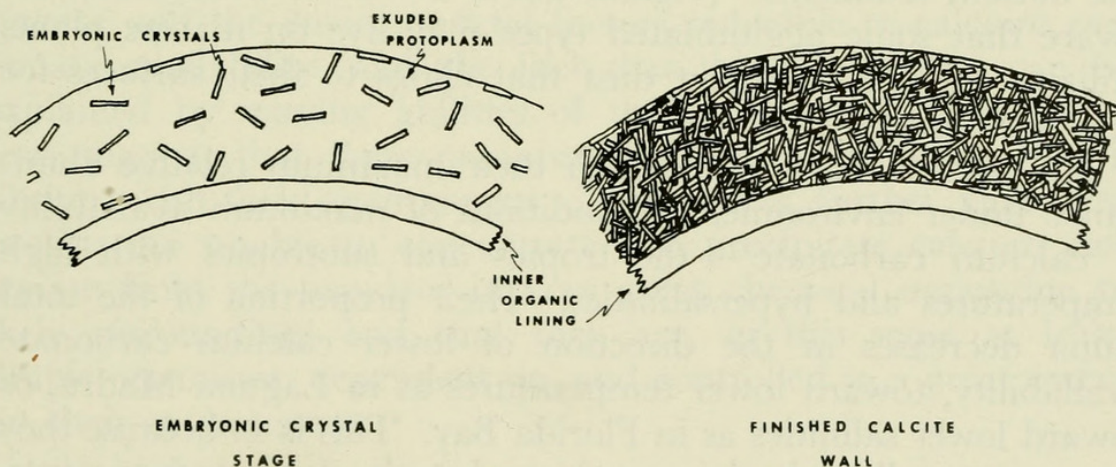


Figure 10. Diagrammatic sketch illustrating differences in test wall calcification in porcelainous and hyaline calcareous Foraminifera. See text for discussion.

cretion of calcite by the porcelaneous Foraminifera dictates that they live within an environment of readily available calcium carbonate — at the point of “saturation” or even “supersaturation.”\*\* The nucleating surface employed by the hyaline calcareous Foraminifera, however, allows them a greater range of habitable environments. Because of this, they can do well both in normal marine and in slightly hypersaline conditions, and are prevented from thriving only within areas of low calcium carbonate availability (usually low salinity) and areas of “hyper-supersaturation” (see below for further discussion).

In the very low salinity environments, where the availability of calcium carbonate is below the threshold required by hyaline calcareous forms, the agglutinated Foraminifera will predominate. This is so simply because the agglutinated species are not restricted by such a boundary, while the calcareous types are. As waters with more readily available calcium carbonate are approached, more hyaline calcareous forms will be present, thus diminishing the relative abundance of agglutinated types. Though the agglutinated types are not excluded from environments of high calcium carbonate availability, they are subordinate in abundance to the calcareous forms there. This can be explained by the ability of calcareous forms to diversify and occupy ecological niches not as readily available to the agglutinated types (*e.g.*, marine plants), as the construction of an agglutinated test ties the protist to its source of raw material — the bottom sediments. (Again, this is a relative situation. I am aware that some agglutinated types may live on marine plants utilizing the fine sediment dust that clings to their surfaces for test construction.)

The porcelaneous types reach their maximum relative abundance under environmental conditions of maximum availability of calcium carbonate — the tropics and subtropics with high temperatures and hypersalinities. Their proportion of the total fauna decreases in the direction of lower calcium carbonate availability, toward lower temperatures as in Laguna Madre, or toward lower salinities as in Florida Bay. This is so because they have greater difficulty in secreting calcite in these environments,

---

\*\*I use the terms “saturation,” “supersaturation,” and “hyper-supersaturation” in a *relative* sense. Though these terms do have definite meanings in chemistry, it is difficult to say at what point a sea-water solution is “saturated” with respect to  $\text{CaCO}_3$  in a natural environment, and even more difficult to state the relation of the foraminiferids to some precise value of saturation. They can be related relatively, however.

while the hyaline calcareous types are seemingly not hindered in this process until very low salinities or temperatures are reached. The porcelaneous types can completely dominate the fauna in environments of very high calcium carbonate availability owing, perhaps, to the unordered crystalline nature of their test walls. Hyaline calcareous types would perhaps be unable to secrete well-ordered crystals in an environment of calcium carbonate "hyper-supersaturation."

Consequently, Foraminifera with hyaline calcareous walls reach their maximum relative abundance in areas of intermediate calcium carbonate availability, where the porcelaneous types are greatly diminished owing to problems of calcite secretion.

*Summary.* An hypothesis has been proposed to explain the observed foraminiferal sequence correlated with salinity and temperature gradients within estuarine environments. The environmental factor thought to control the distributions of major groups is the availability of calcium carbonate utilized in test construction by two of the types. This factor is dependent mainly on temperature, salinity, and  $\text{CO}_2$  content of the water.

This hypothesis adequately explains the observed distributions of these groups; it explains, through physiologic interaction with the environment, the correlation between foraminiferal groups and temperature and salinity gradients; and it ultimately explains the correlation of these groups with climatic factors. The fact that this correlation exists between the foraminiferal sequence and the environmental factors reducible to calcium carbonate availability, and the fact that this relationship can be explained by varying abilities of the foraminifers to construct tests suggest, that these organisms secrete calcite in near-equilibrium with their environment. This implies, further, that these protists are unable to concentrate and precipitate calcium carbonate from the seawater in very great chemical opposition to their surroundings and that they are, in this sense at least, simple organisms, dependent on, and controlled to a great extent by, their environment.

#### GEOLOGIC SIGNIFICANCE OF RESULTS

The understanding of environmental effects on the distribution of organisms and on the modification of phenotypes is essential to the interpretation of paleoenvironments. The purpose of this study has been to gain some understanding of factors governing the distribution of Foraminifera in Recent environments. The

difficulty in learning the causes of distribution of any particular *species* is apparent, and geologic applicability of such knowledge is severely limited by the geologic range of the species. In this light, I have sought to determine the environmental control on a characteristic of the fauna that transcends the specific level of classification and which is amenable to paleoecologic extrapolation. I have shown that Foraminifera are distributed within the Recent environment in a fashion covariant with certain factors summarized as the availability of  $\text{CaCO}_3$ . The proposition that the availability of  $\text{CaCO}_3$  is indeed the cause of their relative abundance distribution is supported by a credible explanation, on the physiologic level, of foraminiferal test construction.

The understanding of distributions at this level depends only on a knowledge of the wall types, not on individual characteristics of a taxonomic group. Much can be learned concerning salinity and temperature distributions in ancient seas and estuaries through use of Foraminifera at this morphologic level. With a more thorough understanding of the causes of planktonic distributions and changes in foraminiferal diversity on the continental shelf, more can be learned of paleobathymetry and location of shore-lines.

Since work with the Foraminifera at this level circumvents the problems associated with extending interpretations of various Recent taxa back in time, application of the principles gained can be extrapolated through the Mesozoic to the beginnings of the calcareous Foraminifera. One major assumption must be made for the interpretation of fossil faunas. This is that the ability of Foraminifera to secrete calcite for particular wall types within a given environment of  $\text{CaCO}_3$  availability has not changed appreciably since the corresponding development of each test type. This assumption, it would seem, is a fair one; if the crystalline structure within the wall of Jurassic porcellaneous Foraminifera is similar to that found in Recent specimens of that wall type, it is reasonable to assume that the physiologic processes that produced it were similar.

Perhaps a more important inference can be drawn from the results of this study. If the Foraminifera depend to such an extent on the availability of  $\text{CaCO}_3$  in specific degrees of saturation or supersaturation within the environment for secretion of their tests, then they cannot readily concentrate these ions physiologically and hence cannot easily act in chemical opposition to their surroundings. This implies further that other aspects of foraminiferal tests are subject to simple control by the environ-

ment. I suggest that such factors as general test morphology, apertural position and number, and chamber number may be governed not strictly genetically (as is implied by the erection of specific or generic groups based on these characters), but by the macro- or microenvironment of the living individual. This, then, is an open avenue for research. If environmental causes for various morphological characteristics can be derived, immeasurable paleoecologic value can be attributed to Foraminifera.

## REFERENCES

- ANGELL, R. D. 1967a. The test structure and composition of the foraminifer *Rosalina Floridana*. J. Protozool., 14: 299-307.
- . 1967b. The process of chamber formation in the foraminifer *Rosalina Floridana* (Cushman). J. Protozool., 14: 566-574.
- ARNOLD, Z. M. 1964. Biological observations on the foraminifer *Spiroculina hyalina* Schulze. Univ. Calif. Pub. Zool., 72: 1-78.
- BANDY, O. L. 1954. Distribution of some shallow-water foraminifera in the Gulf of Mexico. U.S. Geol. Surv. Prof. Pap. 254-F.
- . 1956. Ecology of Foraminifera in the northeast Gulf of Mexico. U. S. G. S. Prof. Paper 274-G.
- . 1964. General correlation of foraminiferal structure with environment. In Imbrie, J., and N. D. Newell (eds.), Approaches to Paleoecology. John Wiley, pp. 75-90.
- AND ARNAL, R. E. 1960. Concepts of foraminiferal paleoecology. Amer. Assoc. Petrol. Geol., Bull. 44: 1921-1932.
- CHAVE, K. E. AND SCHMALZ, R. F. 1966. Carbonate-seawater interactions. Geochim. et Cosmochim. Acta, 30: 1037-1048.
- ESPENSHADE, E. B., JR., ed. 1960. Goode's World Atlas: Rand-McNally.
- FUNNELL, B. M. 1967. Foraminifera and Radiolaria as depth indicators in the marine environment. Marine Geol., Special Issue, 5/6: 33-47.
- GOODELL, H. G. AND GORSLINE, D. S. 1960. A sedimentologic study of Tampa Bay, Florida. Internat'l Geol. Cong., 21st Session, Norden, pt. XXIII.
- GREINER, G. O. G. 1969. Environmental factors causing distributions of Recent Foraminifera. Ph.D. Thesis, Case Western Reserve University, 195 pp.
- . 1970. The distribution of Recent benthonic foraminiferal groups on the Gulf of Mexico continental shelf. Micropaleontology, 16 (1): 83-101.
- HAY, W. H., TOWE, K. M., AND WRIGHT, R. C. 1963. Ultra-microstructure of some selected foraminiferal tests. Micropaleontology, 9: 171-195.
- HEDLEY, R. H. 1963. Cement and iron in the arenaceous Foraminifera. Micropaleontology, 9: 433-441.

- KANE, H. E. 1966. Sediments of Sabine Lake, the Gulf of Mexico, and adjacent water bodies, Texas-Louisiana. *Jour. Sed. Petr.*, **36**: 608-619.
- . 1967. Recent microfaunal biofacies in Sabine Lake and environs, Texas-Louisiana. *Jour. Paleont.* **41**: 947-964.
- LEHMANN, E. P. 1957. Statistical study of Texas Gulf coast Recent foraminiferal facies. *Micropaleontology*, **3**: 325-356.
- LIDZ, L. 1965. Sedimentary environments and foraminiferal parameters: Nantucket Bay, Massachusetts. *Limn. and Oceanog.*, **10**: 392-402.
- LOEBLICH, A. R. AND TAPPAN, H. 1964. Sarcodina, chiefly "Thecamoebians" and Foraminifera. *In* *Treatise on Invertebrate Paleontology, Part C, Protists 2*, v. 1 and 2, R. C. Moore, ed. Lawrence, Kansas: Univ. Kansas and Geol. Soc. America, pp. C55-C164.
- LYNTS, G. W. 1962. Distribution of Recent Foraminifera in Upper Florida Bay and associated sounds. *Contrib. Cush. Found. Foram. Res.* **XIII**, pp. 127-144.
- AND PFISTER, R. M. 1967. Surface ultrastructure of some tests of Recent Foraminifera from the Dry Tortugas, Florida. *J. Protozool.*, **14**: 387-399.
- PARKER, F. L. 1948. Foraminifera of the continental shelf from the Gulf of Maine to Maryland. *Bull. Mus. Comp. Zool.*, **100**: 213-41.
- , PHLEGER, F. B., AND PEIRSON, J. F. 1953. Ecology of Foraminifera from San Antonio Bay and environs, southwest Texas. *Cush. Found. Foram. Res.*, Special Pub. 2.
- PHLEGER, F. B. 1954. Ecology of Foraminifera and associated organisms from Mississippi Sound and environs: *Amer. Assoc. Petrol. Geol., Bull.* **38**: 584-647.
- . 1956. Significance of living foraminiferal populations along the central Texas Coast. *Contrib. Cush. Found. Foram. Res.* **VII**, pp. 106-151.
- . 1960a. Ecology and Distribution of Recent Foraminifera. Baltimore: Johns Hopkins Press.
- . 1960b. Foraminiferal populations in Laguna Madre, Texas. *Sci. Repts. Tohoku Univ.*, 2nd Ser. (Geol.), Special Vol. **4**: 83-91.
- . 1964. Foraminiferal ecology and marine geology: *Marine Geol.*, **1**: 16-43.
- AND PARKER, F. L. 1951. Ecology of Foraminifera, Northwest Gulf of Mexico. *Geol. Soc. America, Memoir* 46.
- REVELLE, R. 1934. Physico-chemical factors affecting the solubility of calcium carbonate in sea water. *Jour. Sed. Petr.*, **4**: 103-110.
- AND FAIRBRIDGE, R. 1957. Carbonates and carbon dioxide. *In* *Treatise on Marine Ecology and Paleoecology*, Vol. 1, Ecology, J. W. Hedgpeth, ed. New York City: Geol. Soc. America, Memoir 67.
- RUSNAK, G. A. 1960. Sediments of Laguna Madre, Texas. *In* *Recent Sediments, Northwest Gulf of Mexico*, F. P. Shepard *et al.*, eds. Tulsa: Amer. Assoc. Petrol. Geol. Pub.
- SHENTON, E. H. 1957. A study of the Foraminifera and sediments of

- Matagorda Bay, Texas. Trans. Gulf Coast Assoc. Geol. Soc., v. VII, pp. 135-150.
- SHEPARD, F. P. AND MOORE, D. G. 1955. Central Texas coast sedimentation: characteristics of sedimentary environment, Recent history, and diagenesis. Amer. Assoc. Petrol. Geol., Bull., 39: 1463-1593.
- AND ———. 1960. Bays of central Texas coast. In Recent Sediments, Northwest Gulf of Mexico, F. P. Shepard, *et al.*, eds. Tulsa: Amer. Assoc. Petrol. Geol. Pub.
- STEHLI, F. G. 1966. Some applications of foraminiferal ecology. Proc. 2nd W. African Micropaleo. Coll. (Ibadan, 1965), pp. 223-240.
- AND CREATH, W. B. 1964. Foraminiferal ratios and regional environments. Amer. Assoc. Petrol. Geol., Bull. 48: 1810-1827.
- THORNBURY, W. D. 1965. Regional Geomorphology of the United States. New York: John Wiley and Sons.
- THORNTHWAITE, C. W. 1948. An approach toward a rational classification of climate. Geog. Rev., 38: 55-94.
- TOWE, K. M. 1967. Wall structure and cementation in *Haplophragmoides canariensis*. Contrib. Cush. Found. Foram. Res. XVIII, pp. 147-152.
- . 1972. Invertebrate shell structure and the organic matrix concept: Biomineralization, 4: 1-13.
- AND CIFELLI, R. 1967. Wall ultrastructure in the calcareous Foraminifera: crystallographic aspects and a model for calcification. Jour. Paleo., 41: 742-762.
- UPSHAW, C. F. AND STEHLI, F. G. 1962. Quantitative biofacies mapping. Amer. Assoc. Petrol. Geol., Bull. 46: 694-699.
- , CREATH, W. B., AND BROOKS, F. L. 1966. Sediments and microfauna off the coasts of Mississippi and adjacent states. Miss. Geol., Econ., and Topo. Surv., Bull. 106.
- WALTON, W. R. 1964. Ecology of benthonic Foraminifera in the Tampa-Sarasota Bay area, Florida. In Papers in Marine Geology, Shepard Commemorative Vol., R. L. Miller, ed. New York: MacMillan.
- WANTLAND, K. E. 1967. Recent benthonic Foraminifera of the British Honduras shelf. Ph.D. Thesis, Rice Univ.

## APPENDIX

### ON THE CONSTRUCTION OF CALCITE WALLS IN FORAMINIFERA

The living calcareous Foraminifera have been divided into two suborders on the basis of general test wall construction: the Miliolina have nonporous, porcelaneous walls; the Rotaliina have a glassy appearance, and are penetrated by numerous pores. Studies with the electron microscope have upheld this basic distinction and have revealed the crystal arrangements underlying and producing this difference, as seen by the light microscope.

The miliolid test wall is composed of two layers of calcite rhombs or needles: an inner, "randomly" oriented layer (which is the thicker) and an outer, pavement-like layer, one rhomb thick, with the rhombs oriented parallel to the surface. The crystallization process in miliolid foraminifers has been observed and reported by Arnold and by Lynts. The process is as follows: Cytoplasm is extruded through the aperture; it then takes on the form of the new chamber. A layer of fibrous organic matter is deposited on the surface of the chamber and will become the "inner organic lining" of the test. After the new aperture is formed, cytoplasm is again extruded, but this time it covers the new chamber in a thin organic sheath, which is to act as the crystallizing matrix.

Mineralization then occurs in two waves of crystal growth, with the rhombs being nucleated either spontaneously or by properly patterned organic molecules, but at many "randomly" placed sites throughout the sheath of matrix. This results in growth of the crystals in a *nonoriented* fashion within an immiscible solvent. This will be contrasted with the result of *oriented* crystal growth in the rotaliids.

Thus the randomly oriented rhombs in the inner layer are the result of randomly oriented crystal nuclei. What special mechanism operates to orient the surface rhombs? I believe this is simply the result of surface tension at the protoplasm-seawater interface, acting on the elongated crystals to align them parallel to that surface. No biological directives are required; it is a simple, physical process. No special crystallizing mechanisms should be sought, and no adaptive significance can be attached to this pavement-like surface layer.

The mineralization process in a hyaline calcareous foraminifer has been watched and reported by Angell, and a mechanism for this process has been proposed by Towe and Cifelli on the basis of the electron microscopic study of test wall sections. The process is as follows: Cytoplasm is extruded through the aperture, and takes on the shape of the chamber to be formed. A fibrous organic layer is secreted to cover the chamber. The cytoplasm is again extruded through the new aperture and covers the new chamber in a thin organic sheath. To this point the process is similar to that of the miliolids, but the fibrous organic layer, which was merely an inner lining for the miliolid, has taken on a new function. It apparently acts as a template for calcite nucleation. Crystallization then takes place beginning on this template, with the calcite crystals growing upward within

the organic sheath. When the process is completed, there are crystals and pores oriented perpendicular to the test surface.

It is my opinion that these pores and crystals are simply the result of oriented crystallization of two immiscible substances from an originally miscible solution — the cytoplasmic sheath. My analysis of the process is as follows: The entire fibrous surface of the new chamber can act as a nucleation template. However, as crystallization commences, both calcite and organic matter are coming out of solution. Since these are immiscible as solids, there will be separation of the two phases. Organic matter will be excluded from the calcite crystal lattice and will migrate toward, and collect in, relatively equally spaced organic plugs on the template surface (the "pore processes" of Angell). As crystallization continues, the same process will result in the upward growth of the two separated phases: calcite will continue to crystallize on calcite, and organic matter on the pore processes. The final result is a wall with oriented calcite crystals, penetrated by organic plugs, which upon death and decay will leave the characteristic "pores" of the hyaline calcareous foraminifers.

The results of the same process can be observed on a macroscopic level, and in an even more convincing manner, in your home refrigerator. Most ice cubes exhibit "pore" structures amazingly similar to those of the hyaline calcareous Foraminifera. They are formed by the entrapment of gases formerly dissolved in the water, which must come out of solution during crystallization. If freezing proceeds from the top down, the gas cannot escape into the atmosphere, and space within the cube must be provided. As crystallization proceeds the water becomes saturated with the gas, and as it comes out of solution, it tends to gather into bubbles at more or less equally spaced sites at the ice surface. This, I am suggesting, is analogous to the separation and collection of organic matter into the "pores" of foraminiferal walls during their mineralization.

The total volume of pore space in the ice cube is dependent on the amount of dissolved gas at the onset of crystallization, but the pore size and density is related to rates of crystallization, as indicated by a few simple experiments which I conducted. The faster the cooling rate of the ice, the smaller, and hence more closely spaced are the pores. This is reasonable, as greater migration of the excluded molecules is possible with slower cooling.

The extension of the original bubbles, and hence the elongation of the pores, is the result of simple physical processes. As

crystallization continues ice will tend to extend already-existing ice crystals, and the gas will collect at sites already occupied by gas. When the entire solution is used up, crystallization stops and the analogy is complete.

Thus "pores" are developed in the crystallization of ice without the need of biologically derived genetic directives, and, I suggest, the same mechanism operates in the calcification of foraminiferal walls. Surely no "adaptive significance" can be ascribed to ice cube pores. Likewise, I believe we err in searching for a "purpose" in the construction of foraminiferal pores. I think the pores are simply the result of the simultaneous crystallization of two immiscible substances upon a nucleation template. Pores do not develop in the porcelaneous walls because nucleation of the calcite crystals is at many sites, scattered throughout the matrix, and exclusion of organic matter from the lattice during crystal growth is accomplished by merely pushing it aside; whereas, in the rotaliid wall, calcite is being nucleated over an entire surface, necessarily forcing the organic matrix to gather at particular sites. Thus, it was the mode of calcification, the organic nucleating surface, which was selected for, and which has adaptive significance, not the "pores." However, this does not exclude the possibility that foraminifers use these "pores" in the quest for specialized adaptations. By increasing the ratio of organic matter to  $\text{CaCO}_3$  (quite possibly through genetic control), it is possible to reduce the calcite wall to a mere lattice work composed almost entirely of pore space, as in the genus *Globigerinoides*, thereby lightening the test in preparation for a planktonic habit. Thus, the very enlarged pores of *Globigerinoides* are in a close-packed condition resulting in hexagonal openings and consequent intervening small triangular calcite pedestals serving as bases for the growth of the spines characteristic of this genus. The spine growth can be simply ascribed to the continued crystallization of calcite in the direction it was started — a common phenomenon in crystal growth.

The factors of pore density and total porosity in recent planktonic Foraminifera have been studied by Bé and are found to be related to environment in a gross way. I suggest that *total* porosity will be related to some factor or factors that govern the matrix to calcite ratio (perhaps this is entirely genetic) and that pore size and density will be found to be related to factors governing rates of crystallization. And this might more closely correlate with environmental parameters. Perhaps in areas of  $\text{CaCO}_3$  supersaturation crystallization will be most rapid, result-

ing in many, minute pores spread over the test, as opposed to larger, more widely spaced pores that might be found in regions of environmentally controlled slow rates of crystallization.

In summary, I would like to emphasize that this is purely a hypothesis for pore formation based on other hypotheses for calcification mechanisms in Foraminifera, and quite possibly the whole matter is more complex than what I have presented here. However, I believe it is important to refresh our thinking by coming to problems from new angles, by making analogies in the biological world with things or processes in the purely physical or chemical world. I especially think that Foraminifera are much less complicated biologically than most workers currently suppose. Much of their activity, their feeding, their shell construction can be duplicated in completely nonbiological systems. Much of their shell morphology is predictable from a purely geometrical point of view; for example, consider the stacking of different sized spheres. Thus, in my opinion, Foraminifera, perhaps more than any other group of organisms, can be utilized in paleoecological studies, because they are basically simple physico-chemical systems; they do not exert much biological pressure against the environment, and hence they are closely governed by the environment; that is, they must work within the confines of molecular forces such as surface tension and crystal growth processes.

Foraminifera must be examined in this new light if we are to advance in our understanding of them. Foraminifera are not molluscs; they do not have their sophisticated biological systems; we must stop looking at them as if they do.



Greiner, Gary O. G. 1974. "Environmental factors controlling the distribution of recent benthonic Foraminifera." *Breviora* 420, 1–35.

**View This Item Online:** <https://www.biodiversitylibrary.org/item/30469>

**Permalink:** <https://www.biodiversitylibrary.org/partpdf/32625>

**Holding Institution**

Harvard University, Museum of Comparative Zoology, Ernst Mayr Library

**Sponsored by**

Harvard University, Museum of Comparative Zoology, Ernst Mayr Library

**Copyright & Reuse**

Copyright Status: In copyright. Digitized with the permission of the rights holder.

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.