Shell Porosity of Recent Planktonic Foraminifera as a Climatic Index

Abstract. *Despite variations in pore diameter and pore concentration between 22 species of planktonic Foraminifera, shell porosites are relatively uniform for those co-occurring in the same latitudinal belts: over 10 percent for tropical-subtropical species; 5 to 10 percent for temperate species; and less than 5 percent for subpolar-polar species. Shell porosities of fossil planktonic Foraminifera may be useful indices for interpreting Cenozoic climates.*

Foraminifera, among the most widespread organisms of the marine plankton, are found at all latitudes of the world's oceans. Faunal groups can be recognized by the co-occurrence of species in particular water-masses and seasons. The individual distributional ranges of Recent planktonic Foraminifera (*1*) indicate that of all 28 species, diversity is greatest in tropical and subtropical waters (22 species), whereas only one species is found predominantly in temperate (transitional) waters, four species in subpolar, and one species in polar regions.

All species identifications depend on the taxonomist's ability to make distinctions based primarily on gross morphology. The shell microstructures of planktonic Foraminifera were investigated to understand their shell growth patterns and to seek refinements in distinguishing living species and genera (*2*). Microstructural features of shells reflect basic growth habits unique to each species, and thus they provide additional taxonomic criteria. When shell growth patterns can be related to the distribution of a species, they can be used to interpret Pleistocene and older marine environmental conditions.

The shells of cold-water planktonic Foraminifera are, on the average, smaller and more compact than those of tropical and subtropical species which display a wide variety of shell forms and surface textures. For example, tropical *Globorotalia menardii* has a smooth shell surface, at least in its early stages, whereas tropical *Globigerinoides sacculifer* is spinose and coarsely textured. When these two species are examined more closely, we see that the smooth surface of *G. menardii* is pierced by many pores of small diameter. In contrast, the coarseness in *G. sacculifer* is due to more widely spaced, large-diameter pores, whose craterlike depressions and surrounding terraced ridges accentuate the surface topography.

To evaluate the significance of shell porosity with respect to environmental interpretation, I measured the pore concentrations and pore diameters of 22 species of Recent planktonic Foraminifera (*3*) from plankton tows and from surface layers of deep-sea sediments, by following a procedure similar to that used by Hofker (*4*), Wiles (*5*), and Berggren (*6*). Hofker's "pore index" refers to the number of pores per unit area and mean pore diameter. Although he has pointed out its taxonomic value in differentiating species, some of his results show a discrepancy with my measurements of certain species (for example, *Globigerina eggeri, G. quinqueloba*, and *G. bulloides*). I examined about 50 specimens of each species and made ten pore-concentration and ten pore-diameter counts on each specimen. The pore concentrations are based on the mean number of pores per 25 $\mu \times 25\ \mu$ square (Table 1). Measurements were made at × 600 magnification on the chamber walls of the last whorl of adult shells (normally longer than 500 microns). In early ontogeny, most species have smaller pore diameters, higher pore concentrations per unit area, and, normally, less shell porosity compared with their adult stages. However, calcification in late ontogeny often produces thick calcite crusts that can greatly reduce or even obliterate the pore openings. Thus, ideally, pore concentrations should be measured on the inner shell surfaces to eliminate the problem of radial divergence of pores

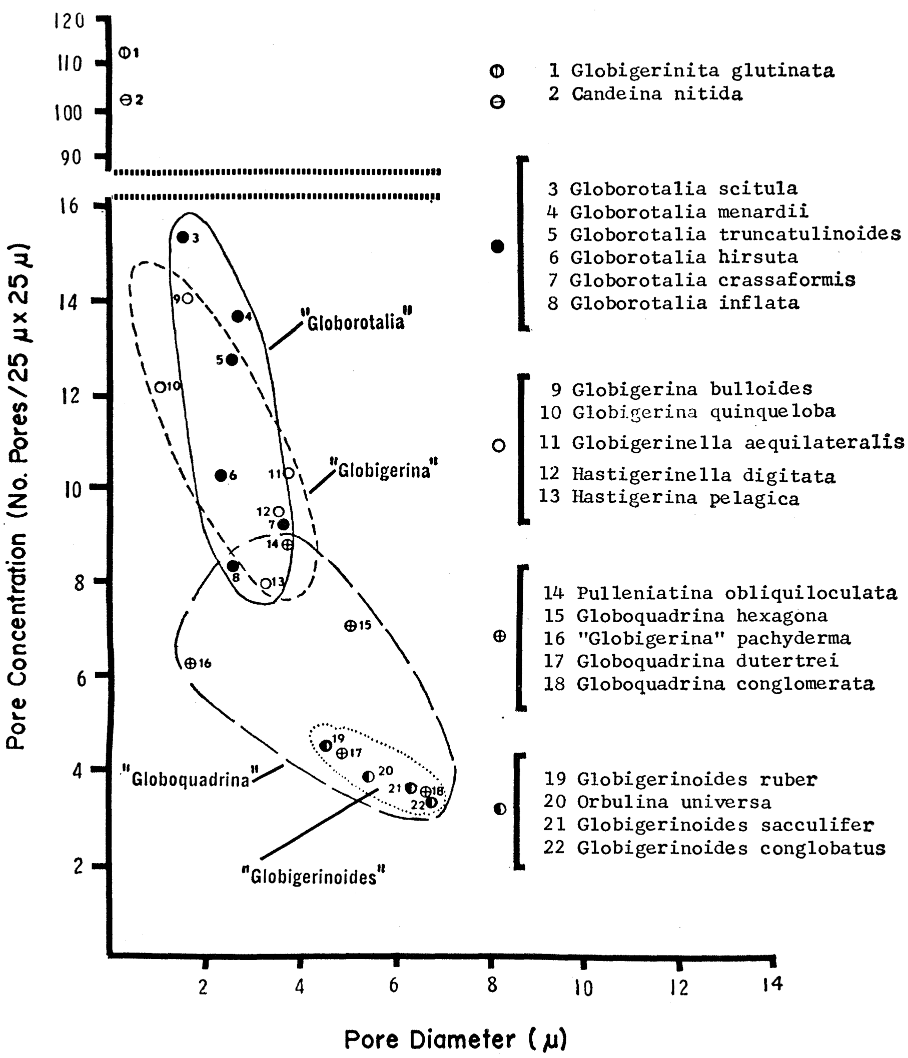

Fig. 1. Mean pore concentration plotted against mean pore diameter for 22 species of planktonic Foraminifera. Four clusters are formed by the major species groups "*Globigerina*," "*Globorotalia*," "*Globoquadrina*," and "*Globigerinoides*," based on similarities in shell microstructures.

Table 1. Twenty-two species of Recent planktonic Foraminifera from plankton tows (0 to 200 m) used for porosity measurements.

Species	**Porosity (%)**	Distributional region	Optimum surf. temp. range (°C)	Locations of samples
Candeina nitida (d'Orbigny)	1.1	Tropical	24–30	13°34'S 33°45'W
Globigerina quinqueloba (Natland)	1.5	Subarctic-Subantarctic	1–12	77°57'N 00°12'E
"Globigerina" pachyderma (Ehrenberg)	2.0	Arctic-Antarctic	0–9	77°57'N 00°12'E
Globigerinita glutinata (Egger)	2.2	Cosmopolitan	3–30	07°31'S 95°19'W
Globorotalia scitula (Brady)	4.3	Subarctic-Subantarctic	4–15	42°07'N 140°31'W
Globigerina bulloides (d'Orbigny)	4.5	Subarctic-Subantarctic	3–19	62°35'N 27°44'W
Globorotalia inflata (d'Orbigny)	7.0	Temperate	13–19	35°04'N 47°59'W
Globorotalia hirsuta (d'Orbigny)	7.4	Subtropical (winter)	17–22	35°04'N 47°59'W
Globorotalia truncatulinoides (d'Orbigny)	9.4	Subtropical (winter)-Temperate	17–22	35°04'N 47°59'W
Hastigerina pelagica (d'Orbigny)	10.1	Subtropical-Tropical	20–26	01°20'S 81°16'W
Globorotalia menardii (d'Orbigny)	11.5	Tropical	20–25	01°20'S 81°16'W
Globigerinoides ruber (d'Orbigny)	11.6	Subtropical	21–29	32°00'N 65°22'W
Hastigerinella digitata (Rhumbler)	13.9	Tropical	20–26	13°31'N 18°03'W
Globorotalia crassaformis (Galloway and Wissler)	14.9	Subtropical	16–27	14°36'S 3°40'E
Pulleniatina obliquiloculata (Parker and Jones)	15.9	Tropical	22–24	37°07'N 69°33'W
Globoquadrina dutertrei (d'Orbigny)	16.2	Subtropical	16–24	05°08'N 42°24'W
Orbulina universa (d'Orbigny)	16.1	Subtropical-Tropical	17–23	05°36'S 85°40'W
Globigerinella aequilateralis (Brady)	16.7	Subtropical	19–28	38°31'N 59°39'W
Globigerinoides sacculifer (Brady)	18.5	Tropical	24–30	19°58'N 68°08'W
Globoquadrina conglomerata (Schwager)	19.6	Tropical	24–30	00°38'S 69°27'E
Globigerinoides conglobatus (Brady)	19.7	Subtropical-Tropical	21–29	13°29'N 58°53'W
Globoquadrina hexagona (Natland)	21.9	Tropical	24–30	16°40'S 78°09'W

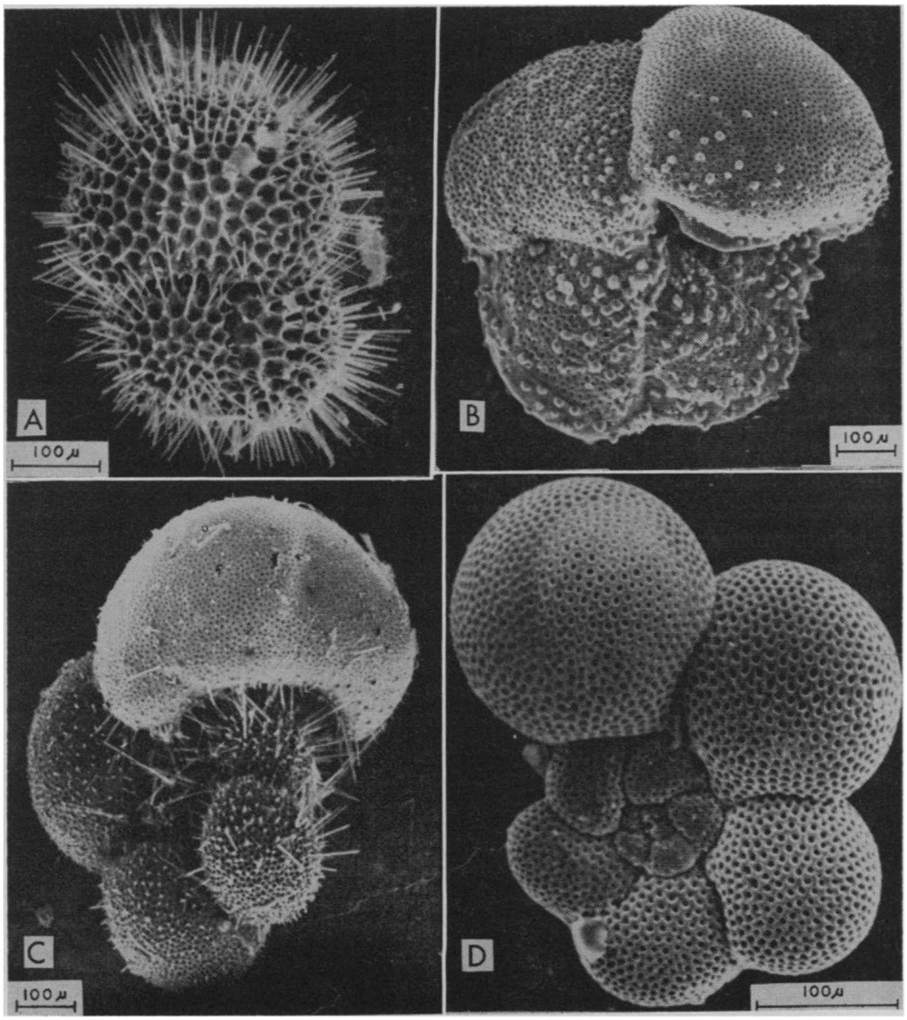

Fig. 2. Representatives of four generic microstructures: (A) *Globigerinoides sacculifer* (Brady); (B) *Globorotalia crassaformis* (Galloway and Wissler); (C) *Globigerinella aequilateralis* (Brady); and (D) *Globoquadrina hexagona* (Natland). Jeolco-JSM-2 scanning electron micrographs.

on the outer surface, and this is especially pertinent for thick-walled specimens.

Pore diameters are more difficult to measure, since the shapes of individual pores vary within a certain range for each species. The cross sections of pores are usually funnel- or vase-shaped for *Globigerinoides* and *Globoquadrina* and cylindrical or barrel-shaped for *Globorotalia,* but variations on the hourglass theme are common in many species. In funnel-shaped pores, the average diameter of the cylindrical section is taken. Because pore diameters vary (for most species they are less than 4 microns), our light-microscope measurements should be regarded as a first approximation of mean pore diameters. Use of the scanning electron microscope should resolve this problem.

Plotting mean ~~pore concentration~~ against mean pore diameter for the 22 species of planktonic Foraminifera reveals a generally inverse relation between these two parameters (Fig. 1). Species with large pore diameters possess few pores per unit area, and the reverse is true for species with small pore diameters. When the values are grouped according to similar shell microstructures of the species, four main generic categories (*"Globorotalia," "Globigerina," "Globoquadrina,"* and *"Globigerinoides"*) (Figs. 1 and 2) are evident, besides the two atypical genera *"Candeina" and "Globigerinita."*

I have placed *Globigerinella aequilateralis, Hastigerinella digitata,* and *Hastigerina pelagica* under *"Globigerina,"* because this group possesses elongate spines and has a finely crystalline shell surface. *"Globigerina" pachyderma* and *Pulleniatina obliquiloculata* lack spines and have a pitted and coarse surface texture in early ontogeny; hence, they belong more properly under the *"Globoquadrina"* group.

The clusters of nonspinose, finely perforate *"Globorotalia"* and spinose, finely perforate *"Globigerina"* overlap closely in Fig. 1. By contrast, the spinose, coarsely perforate *"Globigerinoides"* species coincide at the extreme end of the range of the nonspinose, coarsely perforate *"Globoquadrina"* group. *Globigerinita glutinata* and *Candeina nitida* have extremely high pore concentrations and very minute pore diameters and therefore should be treated as separate groups. These basic differences in concentrations and diameters of pores, which must be reflected in the phylogeny of the planktonic Foraminifera, ought to be considered in tracing their evolutionary lineages.

Mean porosity of the shell walls was calculated for each species in terms of percentage of open pore area per unit of shell area (Fig. 3), that is [(number of pores × mean pore area) / 625 μ^2] × 100. Primary apertures, and the secondary apertures of *Globigerinoides* species, were not taken into account, nor was the significance of porosity considered in terms of the total volume-to-surface area ratio and the shell thickness of each species. The range of observed variations in pore diameters for each species is indicated by the horizontal lines in Fig. 3. For the majority of the species, variations in pore diameter have greater effect upon shell porosity than variations in pore concentrations do.

In comparing the porosity values for the individual species with the isopleths of 2, 5, 10, and 18 percent porosities (Fig. 3), it is evident that the porosity values are related to their latitudinal occurrence; that is, low-latitude species have high porosities and high-latitude species have low porosity values. Regardless of their individual pore concentrations, the polar and subpolar species *"Globigerina" pachyderma, G. quinqueloba, G. bulloides,* and *Globorotalia scitula* seemingly "compensate" by constructing either smaller or larger pore diameters, so that ultimately their porosities are less than 5 percent. Intermediate porosities between 5 and 10 percent are obtained for temperate *Globorotalia inflata,* and two winter species in subtropical waters, *Globorotalia truncatulinoides* and *G. hirsuta.*

High porosities (10.1 to 21.9 percent) were recorded for 13 tropical and subtropical species. They include a wide range of shell types: from the spinose to the nonspinose, from low to high pore concentrations, and from large to small pore diameters. Regardless of variations in pore diameter and pore concentration between individual species, their porosities are uniformly high.

Those having the highest porosities, that is, *Globigerinoides conglobatus, G. sacculifer, Globoquadrina hexagona,* and *G. conglomerata,* are either tropical inhabitants, or surface dwellers, or both. By contrast, *Candeina nitida* and *Globigerinita glutinata* have porosity values of 1.1 and 2.2 percent, respectively. Since the former is a tropical species, its low porosity does not fit the observed pattern of the majority of planktonic Foraminifera. *Globigerinita glutinata* has an unusually wide distribution, occurring in subpolar, subtropical and tropical waters. The extremely minute pore diameters of these two species are the reason for their anomalously low porosity values. The generally large apertures of tropical and subtropical species would yield even greater percentages of open area than are indicated in Fig. 3. The secondary apertures in *Globigerinoides conglobatus, G. sacculifer,* and *G. ruber* would significantly increase their porosities. In contrast, *"Globigerina" pachyderma* and *Globi-*

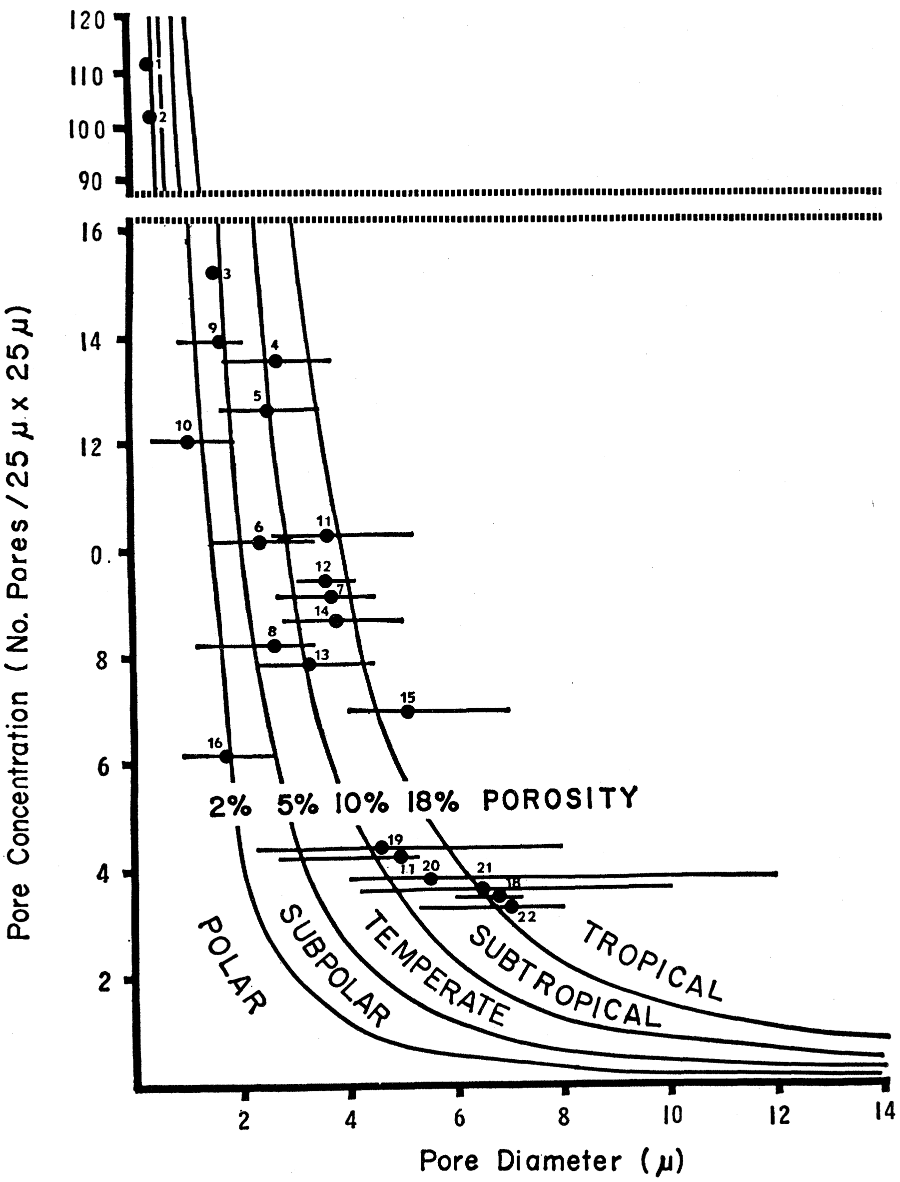

Fig. 3. Shell porosities of 22 species compared to isopleths of 2, 5, 10, and 18 percent porosity and with suggested climatic indices. Numbers refer to species names in Fig. 1. Horizontal lines are observed ranges of pore diameters.

gerina quinqueloba living in polar and subpolar regions have narrow constricted apertures that would not greatly enhance the porosity of their shells. Thus, the omission in my measurements of the open area contributed by apertures would further substantiate the observation that shell porosity can be related to the regional and climatic occurrences of the foraminiferal species.

Wiles (*5*) has demonstrated that variations in the pore concentrations of *Globigerina eggeri* Rhumbler [same as *Globoquadrina dutertrei* (d'Orbigny)] in Atlantic Ocean deep-sea cores can be correlated with Pleistocene climatic changes. His results show that high pore counts were associated with interglacial periods, when tropical-subtropical faunal assemblages prevailed. Low pore concentrations coincided with the glacial ages. Since Wiles did not measure pore diameters, variations in shell porosity of this species could not be determined. If it is assumed that the pore diameters of *G. eggeri* remained relatively constant throughout the core sequences studied by Wiles, then the low pore counts during glacial ages would reduce its shell porosity. Conversely, high pore counts during interglacial times would yield a more porous shell. If this assumption is correct my results would agree with those of Wiles and may perhaps help to explain the climatic influence upon variations in pore concentrations of *G. eggeri*.

The function of the pores in planktonic Foraminifera is little known. They serve as an outlet of the pseudopodia, and it has been suggested (*7*) that they play a role in buoyancy. I propose that the degree of porosity might also be influenced by the availability of light or heat. Planktonic Foraminifera spend their juvenile stages in the upper part of the euphotic zone when their small shells have relatively low porosity. As most species mature below the euphotic zone, the size increase of their shells is accompanied generally by a corresponding increase in shell porosity. Perhaps the lower light intensities at these depths necessitate a more porous shell structure. Calcification in later stages, however, is known to reduce shell porosity to a considerable extent (*2*).

Shell porosities of planktonic foraminiferal species can therefore become useful indices for charting climatic fluctuations during the geological past, as based on the findings that tropical and subtropical species build high-porosity shells and polar and subpolar species construct low-porosity shells.

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Activity Coefficients of Aqueous Sodium Chloride from 15° to 50°C Measured with a Glass Electrode

Abstract. *Values of the mean activity coefficient of sodium chloride at 15°, 25°, 38° and 50°C were determined for aqueous NaCl solutions of 0.01 to 1.0 molal from electromotive force measurements on the cell: (sodium-sensitive glass electrode, aqueous sodium chloride, silver chloride-silver).*

Mean activity coefficients of aqueous sodium chloride ($\gamma_{\pm\text{NaCl}}$) have been determined by means of sodium-amalgam electromotive force (EMF) cells from 0° to 40°C (*1*); by means of concentration cells at 25°C (*2*), from 15° to 45°C (*3*), and from 0° to 50°C (*4*); by boiling-point depression from 60° to 100°C (*5*); and from freezing point data at 25°C (*6*). Most of the values obtained by these methods agree. The relatively new sodium-sensitive glass electrode (*7*) has been used by Lanier to determine the activity coefficient of sodium chloride at 25°C in partially aqueous solutions (*8*) and in concentrated three-component aqueous solutions (*9*). Measurements of $\gamma_{\pm\text{NaCl}}$ in concentrated (1 to 5 molal) NaCl solutions at 0°, 25°, and 50°C have also been reported by Eisenman (*10*). I now report precise measurements of $\gamma_{\pm\text{NaCl}}$ from 15° to 50°C in concentrations from 0.01 to 1.0 molal. The purpose of my investigation was to demonstrate the accuracy of the experimental arrangements in the determination of $\gamma_{\pm\text{NaCl}}$ preliminary to studies of sodium-ion complexes with the same arrangements. The values of $\gamma_{\pm\text{NaCl}}$ at 50°C may be a useful supplement to values obtained in earlier studies.

The cell employed may be represented

$$\text{Na}^{+}\text{-sensitive glass}|\text{NaCl}(m)|\text{AgCl-Ag} \qquad \textbf{(I)}$$

The glass electrode was made by the Corning Glass Company from a glass having the following composition (mole percent): Na_2O, 11; Al_2O_3, 18; and SiO_2, 71. This composition was recommended by Eisenman (*10*) for stability and high Na^+ selectivity relative to K^+ and H^+.

Although potassium-ion interference was not a problem in these experiments, the sensitivity of these electrodes to hydrogen ions limits their range of usefulness in dilute solutions. The hydrogen-ion sensitivity of the sodium-sensitive glass electrode that was used in these experiments is relatively low. The EMF of the Corning electrode in 0.1 molal NaCl is unaffected by hydrogen ion for *p*H values greater than 4.5 and the effect at *p*H 4 is only 1.2 mv. The hydrogen-ion effect on other sodium-sensitive glass electrodes is 2 to 20 times greater (*11*).

The AgCl-Ag electrodes were of the thermal-electrolytic type (*12*). Several electrodes were prepared simultaneously, and those with bias potentials greater than 0.03 mv were rejected. These electrodes proved satisfactorily stable in dilute NaCl solutions and, provided the solution was already saturated with AgCl, in concentrated solutions as well.

The reagent grade NaCl used was dried but was not otherwise purified, because the electrodes are unaffected